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A REVISION OF THE NORTH AMERICAN ANNELID WORMS OF THE GENUS CAMBARINCOLA (OLIGOCHAETA : BRANCHIOBDELLIDAE)

By RICHARD L. HOFFMAN

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A REVISION OF THE NORTH AMERICAN ANNELID WORMS OF THE GENUS CAMBARINCOLA (OLIGOCHAETA: BRANCHIOBDELLIDAE)

By Richard L. Hoffman[1]

Introduction

The annelid worms of the oligochaete family Branchiobdellidae are for several reasons of more than casual interest to the zoologist. Owing to their singular mode of life as commensal or subparasitic inhabitants of freshwater crayfish throughout the Northern Hemisphere, they have departed in numerous respects from the more typical families of the order, and have developed such a leech-like habitus and appearance that for many years the Branchiobdellidae was thought to be a family in the Hirudinea. The problem remains unanswered: is the similarity of the two groups due to convergence influenced by environmental factors, or do the oligochaetes represent a way station along the evolutionary path taken by leeches? The life history has been worked out for none of the species, nor do we know more than a few inferential details about the distribution of any of them. Branchiobdellids should compel the interest of investigators

[1] Department of Biology, Radford College, Radford, Virgina.

if for no other reason than the position of the group on the borderline between commensalism and true parasitism, which ought to provide good clues about the evolution of the latter. It is obvious, however, that such studies can hardly be made until the classification of the group has been worked out, and specific identities firmly established. So far, no extensive work has been done in this direction.

The present study was rather in the nature of a test to see if the species of a widespread and somewhat heterogeneous branchiobdellid genus might be defined on the basis of such characters of the reproductive systems as have been found reliable in many other groups of invertebrate animals. Traditionally, genera as well as species in the Branchiobdellidae have been based on such characters as body form, shape of the jaws, even size of the animals. Clearly it would not take long to exhaust the possible combinations of such features, and by 1950 the taxonomy of American branchiobdellids had reached virtually an impasse. The major consideration underlying this investigation, therefore, has been the determination of what constitutes a species in the genus *Cambarincola*, and the development of coherent diagnoses by which these units may be subsequently identified. I feel that these objectives have been achieved with a fair measure of success.

An inquiry into characters of systematic value reveals that the most important appear to be the gross form as well as histological nature of the spermiducal gland and the adjoining prostate gland, and that these structures afford the basis for division of the genus into sections and groups. The two largest sections seem mainly to be composed of structurally generalized species on one hand and presumably more specialized forms on the other. That a satisfactory grouping of species into a system approximating the evolutionary or phylogenetic trends within the genus has been established is by no means asserted, however. That future studies will impose changes and modifications seems inevitable, yet a start must be made!

The species of *Cambarincola*, as now defined on the basis of the male reproductive organs, are remarkably constant for soft-bodied animals, and well-preserved material can be identified with virtually 100 percent confidence. Most of the species that are known from sufficient material are structurally uniform over their entire area of distribution, and the geographic ranges are in all cases entirely consistent with established biotic or physiographic provinces. The continent-wide distributions published by previous workers are largely the result of misidentifications.

In addition to the purely taxonomic aspect of this work, it has been possible to draw some inferences from present knowledge of structure

and distributions concerning evolution in the group as well as the possible routes by which branchiobdellids settled the North American land-mass. I suspect that the worms came to this continent probably in late Cretaceous times on primitive astacine crayfish from eastern Asia, and that these crustaceans may have spread eastward across the continent—giving rise to the more specialized cambarine genera in eastern North America rather than in Mexico as postulated by students of the Decapoda. The present discontinuity in the distribution of *Cambarincola*, and the isolated, relict status of its most primitive forms, are thought to be the result of fragmentation of the old habitat conditions by climatic changes in the late Tertiary.

Acknowledgments

This study of *Cambarincola* was made at the suggestion, and under the sympathetic guidance of Dr. P. C. Holt. I take great pleasure in acknowledging the extent of his personal interest and concern in facilitating and furthering my investigations, always more in the role of longtime friend than that of major professor. The work was done while I was a candidate for the Ph. D. degree in the Graduate School of the Virginia Polytechnic Institute. Financial support was furnished by a research grant (G–4439) to Dr. Holt from the National Science Foundation.

I am likewise under an obligation to Dr. Fenner A. Chace, Curator of the Division of Marine Invertebrates, U.S. National Museum, who provided working space and the opportunity to study type specimens, and later kindly loaned the bulk of the Museum's holdings in branchiobdellids for study.

It is finally necessary to acknowledge the contribution of numerous collectors who have obtained the material with either a direct or indirect interest in branchiobdellids, particularly Mr. C. W. Hart, who made a special effort to obtain topotypes of *Astacobdella philadelphica*.

Review of the Literature

The first American species of *Cambarincola* to be described was placed in the genus *Astacobdella*, a group of Palearctic leeches (Leidy, 1851). Since that time, the generic concept has been slowly but progressively refined.

In 1894, J. P. Moore described several new species of branchiobdellids from eastern United States, and in his paper discussed Leidy's earlier name under the combination *Branchiobdella philadelphica*, and published an outline drawing of a specimen. The majority of Moore's work on this group involved species of other genera, although in a brief reference in his paper on the leeches of Illinois (1901) he

created the new combination *Bdellodrilus philadelphicus*. There is, of course, little close affinity between *philadelphica* and *Bdellodrilus illuminatus*.

Thus, by the beginning of the present century, only a single species of *Cambarincola* had been described among the total of six branchiobdellids then known from America. In 1912 a new impetus to the study of the group came in the form of two important papers. One of these was a synopsis of the entire family by Umberto Pierantoni, which listed all of the species known to him up to that time, and included the description of a new species, *Branchiobdella americana*, from Texas and North Carolina. This form is almost certainly a species of *Cambarincola* as the genus is defined today. Almost simultaneously, a short paper was published by Max M. Ellis in which *Cambarincola* was established as a new genus for the reception of the new species *macrodonta* from Colorado.

The description of *macrodonta* is a good one, and includes illustrations of the jaws and a partial diagram of the male reproductive system. Comparison was made largely with *philadelphica*, which was one of the originally included species, and which was differentiated largely on the basis of peristomial characters.

During the next several years, Ellis accumulated data from his own collections and that of the U.S. National Museum. In 1918 he published a brief annotated list of branchiobdellids obtained in northern Michigan, and provided a key for their identification. This treatment included *Cambarincola philadelphica* and a new species called *C. vitrea*, although the latter was not formally described and the notation was made that a complete description was then in press. In the following year appeared Ellis's major work, a summary of the branchiobdellid material of the U.S. National Museum. This paper included a discussion of variability in various systematic characters, photographs of entire animals, and the descriptions of several new genera and species. A key was given for the known forms of *Cambarincola*, with notes and records on established species and full descriptions of *C. vitrea*, *C. inversa*, and *C. chirocephala*, the last two names published for the first time.

Following the appearance of this useful paper, Ellis diverted his interests into other channels, and the systematic study of our branchiobdellid fauna languished for several decades. During the last years of the 1930's, Clarence J. Goodnight took up the study of the group, publishing several papers between 1939 and 1943. His major work is a synopsis of the North American branchiobdellids, which appeared in 1940. Here he accounted for 21 species in 9 genera, with 4 of the species being described as new. Insofar as *Cambarincola* was concerned, Goodnight admitted the genus in virtually the same sense as

did Ellis. It was placed in the new subfamily Cambarincolinae with 7 other genera and, in the key to these genera, placed next to *Xironogiton*, solely on the basis of having an "accessory sperm tube" (actually this structure is not present in *Xironogiton* at all). *Cambarincola* was then divided into two subgenera following the initial dichotomy in the key of Ellis (1919, p. 256), with species in which the "upper lip" is entire composing the nominate subgenus, and those with lobed peristomata forming a new subgenus *Coronata* which was set up for *philadelphica* and *chirocephala*. In the subgenus *Cambarincola*, the typical species *macrodonta* was associated with *inversa* and *vitrea* of Ellis, and a new species named *C. elevata*. Recent study has indicated that both *inversa* and *elevata* are members of quite different genera.

Subsequent to the appearance of his monograph, Dr. Goodnight published three additional short papers in which new species of *Cambarincola* were described: *C. floridana* in 1941, *C. meyeri* in 1942, and *C. macrocephala* in 1943. In his 1941 paper on the branchiobdellids of Florida, Goodnight listed four species for the State.

In 1947, the study of branchiobdellids was taken up by Perry C. Holt, and his Master's thesis, published in 1949, treated the comparative morphology of two species (*Xironogiton instabilius* and *Cambarincola philadelphica*) with respect to the male reproductive systems. From the detailed findings of this study, it became evident that the sexual organs, previously only casually mentioned in print, represent a source of the first magnitude for taxonomic characters. Holt's doctoral dissertation dealt primarily with other branchiobdellid genera, but included notes and studies on *Cambarincola*, and two of the new species recognized were subsequently published under the names *C. branchiophila* (1954) and *C. macbaini* (1955).

With the recent accumulation of extensive collections of specimens from many localities, it has become possible to undertake extensive systematic studies on American branchiobdellids, and as a preliminary step in an overall general program, the holotype and paratypes of *Cambarincola macrodonta* were restudied and the genus and species redefined in a short paper published by Holt and Hoffman (1959).

Two of the most important papers recently published by Holt treat the taxonomy and morphology of the genera *Ceratodrilus* (1960a) and *Ellisodrilus* (1960b).

Names and Type Specimens

In general, the overall validity and stability of any systematic revision increases proportionately to the number of type specimens examined. This is nowhere more true than in the case of the family Branchiobdellidae, inasmuch as very few of the published descriptions

are at all explicit concerning details which now must be known for the identification of species in the family.

I have discovered that *Cambarincola* has become something of a catch-all name which has been stretched to cover a wide diversity of species since its original proposal. So far, 13 species have been named in the genus, listed chronologically as follows:

C. philadelphica (Leidy, 1851)
C. macrodonta Ellis, 1912
C. vitrea Ellis, 1918
C. chirocephala Ellis, 1919
C. inversa Ellis, 1919
C. okadai Yamaguchi, 1933
C. elevata Goodnight, 1940
C. floridana Goodnight, 1941
C. meyeri Goodnight, 1942
C. macrocephela (sic) Goodnight, 1943
C. gracilis Robinson, 1954
C. branchiophila Holt, 1954
C. macbaini Holt, 1955

Of the above names, I have seen the type specimens of all but two: *philadelphica* and *okadai.* If Joseph Leidy prepared slides of his specimens, their present location is unknown. The specific concept of *philadelphica* here adopted was derived from topotype specimens, kindly obtained in Philadelphia by Mr. C. W. Hart, which agree in every particular with the original description. Information on *C. okadai* has been limited to what can be deduced from the description. Types of the remaining 11 species are in the collection of the Division of Marine Invertebrates, U.S. National Museum, and have been studied through the kindness of Dr. Fenner A. Chace.

On the basis of the generic concept developed during the course of this study, it has been determined that several of the foregoing species do not belong in *Cambarincola* as now defined. These are:

C. inversa Ellis: This species differs from *C. macrodonta* in details of the bursa and in lacking a prostate gland, as well as in the form of the jaws. Only the type slide has been available for study, but it is evident that *inversa* belongs to a different, as yet undefined genus.

C. elevata Goodnight: The internal structure cannot be seen in the poorly mounted holotype, but the recent examination of topotype material shows that this species likewise is not congeneric with *macrodonta,* and is being included instead in a new genus being readied for publication by Dr. Holt.

C. macbaini Holt: This species, and some others as yet unnamed, differs strikingly from the cambarincoloid forms in having a very long, filiform, protrusible penis, and forms the basis of another new genus soon to be proposed.

With these deletions, the number of valid forms in the genus to the present is reduced to 10. The examination of a great number of specimens in the Holt collection has disclosed a fair number of the described species (6 of the 10) and even more undescribed forms, of which 12 are named in the following pages. The type specimens of

these species are deposited in the U.S. National Museum, with paratypes retained by Dr. Holt.

In addition to the names in the preceding list, one other must be recognized as a probable member of the genus. This is the species described in 1912 as *Branchiobdella americana* Pierantoni. The description is not adequate for recognition of the species, and was probably composite in being based on specimens from Texas and from North Carolina. Until Pierantoni's material can be restudied and a lectotype designated, the status of this name remains in doubt, but the chances are good that it is based on specimens of *Cambarincola*.

Material Examined

The following summary of *Cambarincola* is based upon the examination of about 900 collections of branchiobdellids, some 800 of which contained species of this genus. Over 1100 individual slide mounts have been examined, each with an average of about eight worms per slide. Thus, approximately 9000 specimens of *Cambarincola* have actually been examined closely for structural details, and yet another thousand have been handled while sorting preserved material prior to making slides.

At least 90 percent of all this material is in the private collection of Dr. Perry C. Holt, now housed at the Virginia Polytechnic Institute. In addition, I have been able to examine the portion of the collection of Max M. Ellis which was turned over to the U.S. National Museum. These two sources constitute virtually all the specimens of branchiobdellids now available in North America.

Of the 22 species now accounted within the limits of the genus, I have been able to examine the types of all but two, as well as the type material of various other species described as *Cambarincola* but properly referable to other genera. All the existing holotypes are in the National Museum, paratypes of about half of the species are in the Holt collection.

Methods of Preparation and Study

Although the structure of the reproductive systems undoubtedly provides the best criteria by which species may be defined and their affinities established, it requires far more careful observation and study than has previously been expended in the mere determination of body form and jaw shape; the aspiring student of the Branchiobdellidae must be warned that the group is not one that can be comprehended with a few weeks of attention. The preparation of material for study is not difficult, but observation of the internal characters of even well-mounted specimens is almost always tedious. Probably a

year of continuous study is the minimum prerequisite for any sort of competence in the systematic study of the group.

Only well-preserved and accurately labeled material should be utilized. 80 or 90 percent alcohol (which may include 1 percent of a stock formalin solution) is suggested for initial preservation, and the collector should avoid overcrowding the jar with crayfish. Too many of the crustaceans in one container dilute the preservative and cause maceration of the worms. Isopropyl alcohol may be used, full strength, for preservation, although it is usually only about 70 percent in strength, and fewer crayfish can be placed in a given volume.

Material so preserved may be left indefinitely in jars with the host animals or isolated and restored in tiny shell vials plugged with cotton and packed in larger jars. Each collection may be assigned a different number which relates the specimen vial to collection data entered in a book or on index cards. Either the collection number alone, or a tiny label printed with a fine pen, will suffice to be included in the vial. Cataloging systems are limited only by the ingenuity of the individual, but in practice, the simpler a system the better.

In curating material, one removes the crayfish from the jars with enough vigorous shaking to dislodge any worms that may be still attached to the exoskeleton. It is also desirable to search the branchial chambers and gill filaments for gill-inhabiting forms, either by cutting open the carapace with stout scissors or by extracting the gills with a curved-tip forceps inserted between the carapace and bases of the legs. The gill material is then placed in a dish of alcohol and picked apart under a low-power dissecting microscope. This done, the majority of the alcohol is decanted carefully from the collecting jar to avoid loss of any of the bottom sediment which is then transferred to a flat glass dish and examined with a dissecting microscope.

In a given collection there may be but a single species or as many as four, each representing a different genus. As a rule these species will differ enough in habit form to facilitate easy separation, although in some cases identification even to genus is difficult until slides are prepared. In practice it is advisable to select good specimens of each form for mounting, all of which can be processed together. From the flat-bodied forms such as the species of *Xironogiton* and *Xironodrilus*, it is desirable to choose specimens which are least curled or twisted. From the cylindrical forms, which normally preserve in a sort of crescent-shaped profile, one should select those which are most nearly straight in the plane of the dorsoventral median body axis. Since knowledge of the jaw form is important, it is useful to prepare at least one specimen flattened dorsoventrally, or to remove the head from a specimen and split it along one side to allow for subsequent spreading at the time of mounting. This operation is easily done with a fine-

tipped scalpel or fragment of razor blade mounted in the end of a matchstick. In very large specimens (over 5.0 mm. long when preserved), it is often difficult to observe the reproductive system in whole mounts, and with a little practice it is easy to bisect the body between segments VI and VII, and then dissect out the male organs to be dehydrated and cleared separately.

Processing can easily be done in small glass dishes or similar containers. For ordinary whole mounts it is satisfactory to take specimens from the collecting jar into 95 percent alcohol, then through one change of absolute alcohol into clove oil. About 10 minutes in each stage is sufficient. All the material from each collection can be carried along in the same container, the fluids being added from dropping bottles and removed by a fine-tipped pipette.

Specimens may be mounted singly on each slide, or all of those which look alike mounted together, although this sometimes results in several species on a slide. I have used fairly thick balsam in a drop at the middle of the slide, subsequently spread out by the addition of a little clove oil around its base. Cleared specimens are removed from the clove oil with forceps or a bent needle and placed in the balsam, with specimens about equally divided according to which side is uppermost (to insure having at least one with the reproductive systems on the upper side). If dissected heads are involved, they can be spread in thicker balsam with the jaws uppermost and the coverslip applied quickly.

Slides in the Holt collection are prepared with the mount in the middle, leaving space for the catalog number and/or locality data label at the right end, and for an eventual determination label at the left. Following identification, an index card may be made out with the species name, number, and collection data, and filed in systematic order. Since a slide may contain several species, it is preferable that slides be stored in simple numerical order.

In the study of specimens, the use of medium high power magnification is mandatory, with a range of from about 60 to 600 diameters most desirable. Most of the present study has been made with a fluorite oil immersion objective, 40×,N.A. 100, corrected to a working distance of 1.5 mm., permitting the examination of relatively thick preparations inaccessible to the ordinary high dry and oil-immersion objectives.

Drawings are easily made with a camera lucida attachment, and measurements with a calibrated ocular micrometer.

In many instances, the student will find it impossible to determine single specimens with confidence. Contents of the gut may be so opaque as to conceal the sex organs, or the jaws may be in an unsatisfactory position. Specimens preserved in weak alcohol may be

macerated internally. Sometimes thick or opaque specimens can be utilized by turning the slide over and focusing on the other side of the animal, or by dissolving the balsam away in clove oil or xylol and remounting.

Very small animals, or those with complicated reproductive systems, must sometimes be imbedded in paraffin and sectioned. Well-known histological techniques, using a hematoxylin-eosin stain, suffice for serial sections. I have found no advantage in staining specimens for whole mounts.

Often it will be found necessary to derive specific characters from several specimens, there being few mounts in which all the desired details can be seen on a single animal.

Taxonomic Characters

The taxonomic utility of various anatomical systems in the Branchiobdellidae has been discussed in the literature at least four times. Insofar as earlier workers were concerned, general body form and shape of the jaws provided sufficient basis for the recognition of species, an opinion which unfortunately has survived in some quarters nearly down to the present time. That internal anatomy might furnish characters of really fundamental importance was first intimated by the still unsurpassed account of *Bdellodrilus illuminatus* by J. Percy Moore in 1895. Almost two decades later, Ellis (1912) relied to some extent on the form of the male reproductive systems in the diagnosis of his *Cambarincola macrodonta*, but in his subsequent work of 1919, Ellis largely reverted to nonsexual characters in the definition of genera and species. In this practice he was followed by C. J. Goodnight, and not until 1949 was the study of reproductive morphology revived by Perry C. Holt. Subsequent work by Holt, and that done under his direction by the present investigator, has been predicated upon the assumption that characters of the male reproductive systems provide the most reliable indices of evolution within the group, and, therefore, the best means for the definition of species and genera.

Ellis (1919) devoted considerable attention to the form of the jaws, the nomenclature of their dentition, and their mode of evolution, as well as to pharyngeal diverticula, intersegmental septa, and form of the gut. No further treatment of taxonomic characters appeared until 1935, when Yamaguchi provided a detailed consideration of various useful details, including the body form and ornamentation, jaw structure, and the internal characters mentioned by Ellis. Yamaguchi also discussed variations in the reproductive systems, but not in as much detail as might be desired.

Goodnight's monograph of 1940 reviewed the work of both Ellis and Yamaguchi, as well as several of their predecessors, and en-

deavored to evaluate the systematic value of the previously used characters. Goodnight, however, added little to our knowledge of this general subject, and his references to the structure of the sexual organs are meager. Finally, on the basis of his own knowledge of branchiobdellid anatomy, Holt (1953) published a review of previous work, and introduced information compelling greater attention to the reproductive systems.

The following discussion of anatomical characters which appear to be of taxonomic significance summarizes the points of interest which have been considered during the study of *Cambarincola* and related genera. It has been found necessary to review each character regarding its development in the family at large, and then particularly as it occurs within the more circumscribed limits of *Cambarincola*.

I. Body Form

Branchiobdellids vary greatly in form, but the typical appearance is that of an elongate fusiform cylinder, with a distinctly set-off head and a caudal sucker, both of variable dimensions but normally smaller than the head. In general each body segment is composed of two subsegments, of which the posterior is usually a little larger in diameter than the other. Several variations from this form occur: in *Xironogiton, Xironodrilus*, and some related genera not yet formally segregated from the latter, the body is strongly compressed dorsoventrally, broadest near the caudal end. In *Xironogiton* the body outline is unusual in being very abruptly narrowed anteriorly, having something of the shape of a tennis racket. In the poorly known genus *Triannulata*, each body segment is said to have three subsegments instead of two, although an approach to that condition occurs in the large species *Cambarincola macrocephala*. A terete body such as described in the first sentence characterizes most species of branchiobdellids, including all *Cambarincola*, and is probably the primitive condition in the family. Flattened bodies are doubtless specializations, although genera so formed are not always specialized in other particulars.

II. Body Size

Owing to the normally extensive degree of contractability characteristic of most oligochaetes, the subject of body size and proportions is not an easy one to treat satisfactorily. Branchiobdellids in life are able to double or halve their normal length during motion, and preserved and contracted specimens give an inadequate idea of the living animal. Yet with proper preservation, contraction is not excessive and species can be compared in general terms of relative size. Known species in the family range from about 1 mm. up to 18 mm. or more in length. Intraspecific variation tends to increase

with increase in size; smaller species usually remain within very close limits to their average. The range in size in *Cambarincola* is as great as for the rest of the family, with no particular affinities being reflected by the development of very large or very small forms, both of which occur in groups unrelated by other characters. Both size extremes appear to occur only in mountainous regions, whereas species of moderate dimensions tend to be widespread in lowland areas. In general, so far as *Cambarincola* is concerned, body size is often a good specific character, usually associated with other structural features, and is sometimes useful in identification.

III. Body Ornamentation

The vast majority of branchiobdellids are basically similar in external appearance, but in several forms the segments are provided with dorsal elaborations in the form of fleshy digitiform lobes of various length, or even large median processes which are distally branched. Species so ornamented have traditionally been thrown into the genus *Pterodrilus* without any consideration of other characters, and that "genus" has become a sort of assemblage of incongruous forms most of which are quite unrelated.

In many species the peristomium is produced into four lobes of variable size and length on the dorsal side. These structures reach their maximum development (among American species) in the genus *Ceratodrilus*, becoming nearly as long as the head. In *Cambarincola*, lobation of the peristomium occurs in various forms, and has been used and misused in the past for separation of species and subgenera, even though the significance of the character has been misunderstood. *Cambarincola philadelphica* has been considered by both Ellis and Goodnight to be very variable in this respect, but in actuality the variation ascribed to that species is due to a confusion of several distinct species under one name. Well defined peristomial lobes ("tentacles") occur in association with other characters and reflect specific distinctness of worms so endowed. They do not alone indicate relationships, however, for they occur in several groups of the genus *Cambarincola* as well as in *Ceratodrilus* and *Stephanodrilus*.

IV. Jaws

Branchiobdellids are the only Oligochaeta having sclerotized mouthparts (in the form of a dorsal and a ventral piece) of variable size and shape, but generally provided with caudally directed dentations or cusps on the posterior margins. (The name "jaw" is used only provisionally for the buccal armature of branchiobdellids, with the realization that it is certainly not homologous even with the mouthparts of polychaetes.) Ellis (1919) postulated that the

primitive condition involves subequal jaws in which the cusps are similar in size and shape, and that specialization influences enlargement of the median tooth of the upper jaw. He devised a system of nomenclature to reflect size order of the teeth, and is responsible for the term "dental formula" by which the number of teeth can be stated numerically (e.g., 5–4), indicating that the upper jaw has a median tooth and two more on each side while the lower jaw has two paramedian teeth plus one lateral cusp on each side. However, other arrangements are common, particularly in Oriental species. The American *Ceratodrilus* has small transverse jaws each with 6 to 8 equal dentations, and genera such as *Xironogiton* are likewise small-jawed but usually with a smaller number of teeth. Ellis studied variation in the jaws of what he considered to be *Cambarincola philadelphica* and found considerable individual variation, although it is now known that he had confused several species under that name.

Insofar as *Cambarincola* is concerned, there is considerable latitude in the ranges of variation, individual and geographic as well as specific. Individual variation is largely a function of age, with small specimens of a species having proportionately larger jaws in relation to head size, with more acute dentations. Older specimens tend to have the lateral cusps obscured or worn away. Geographic variation affects the relative length of the jaws in such species as *Cambarincola vitrea*.

The typical jaw arrangement in the genus is one of essentially equal-sized jaws, the dorsal with a large median tooth and two or four small lateral cusps, and the ventral jaw with two large paramedian terminal teeth and a pair of small lateral dentations. Various departures from this basic pattern occur, however, affecting both the relative size and dental formulae, and a rough classification can be drawn up as follows:

Jaws isomorphic, having the same outline in dorsal aspect, and the dental formula 5–5 or 3–3. In lateral aspect, the jaws are mirror images. The species so characterized can be called "homognathous," and they occur sporadically in different sections of the genus. *C. faliax* is a good example.

Jaws anisomorphic, being dissimilar in armature, the dental formula being 5–4 or some other combination of odd and even numbers. This general class is further divisible according to the relative size and shape of the teeth.

Teeth virtually subequal, presumably the primitive condition, occurring in *C. vitrea* and some related forms. Such species are "homodontous."

Teeth dissimilar, the median dorsal and paramedian ventral dentations enlarged, this being the most typical condition in the genus, and can once more be divided according to the relative size of the jaws:

Jaws similar in size in both lateral and dorsal aspects, this including the majority of species such as *C. philadelphica, macrodonta, ingens,* etc.

Jaws markedly dissimilar in size, the dorsal jaw up to four or five times as bulky as the ventral. This is presumably an advanced stage of specialization, and species so characterized may be called "heterognathous."

V. Male Reproductive System

The various species of Branchiobdellidae depart but slightly from a basic organization of the reproductive organs. The function of producing spermatozoa and collecting and conveying them to the exterior is accomplished by the same organs and structures in all members of the family, although the individual parts of the system are subject to variations which, when considered collectively, afford a fair opportunity for systematic diversification. The genital systems of species in the genera *Bdellodrilus* (Moore, 1895b), *Xironogiton* and *Cambarincola* (Holt, 1949), and *Ceratodrilus* and *Ellisodrilus* (Holt, 1960a, 1960b) have already been elucidated in print. The treatment of *Ceratodrilus* is of particular interest in providing a standardized and morphologically correct terminology to replace the various haphazard names which have been used or misused by previous workers. The following terminology is that developed by Holt (1960a). The sequence of the reproductive organs proceeds in order from the testes outward. Reference may profitably be made to the accompanying diagrammatic representation (figs. 1 and 2) of the arrangement.

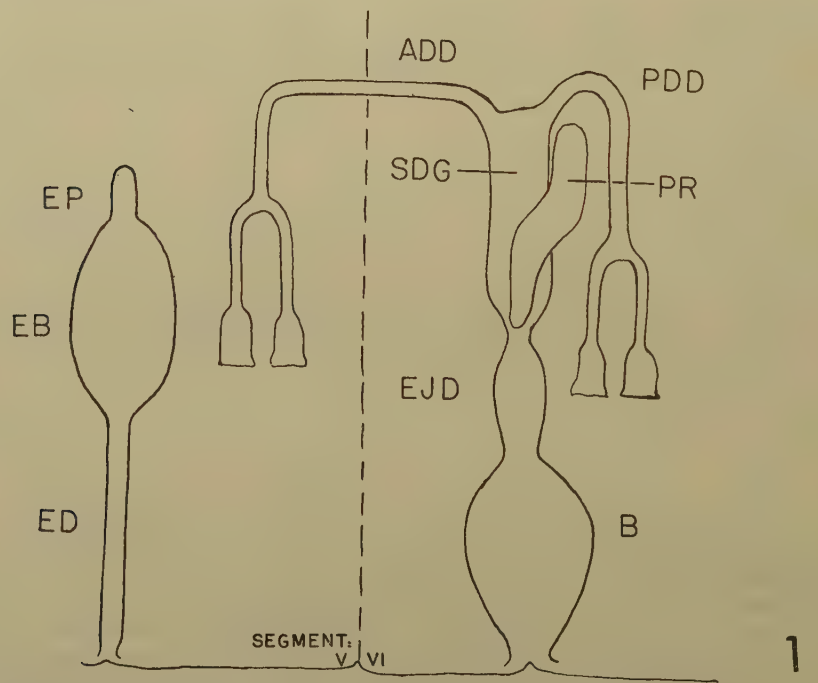


Figure 1.—Diagrammatic representation of the organs, other parts, and nomenclature of the reproductive systems in *Cambarincola*. (For explanation of abbreviations see figs. 2–5, p. 288.)

Testes. The spermatogenic tissue of branchiobdellids is concentrated into one or two pairs of testes located on the posterior face of segmental septa 4/5 and 5/6, or only on 5/6. As a rule the testes are perceptible as such only in immature animals, sexually mature adults show the condition in which the gonads have liberated morulae into the coelom, the fluid of which becomes filled with masses of spermatozoa and disintegrating blastophore material. As a rule, however, the sperm masses are easy to observe in most whole mounts, particularly as they tend to become oriented in clusters before the openings of the funnels, and provide evidence concerning the distribution of the testes. At least one genus (*Branchiobdella*) is provided with testes only in segment VI, a condition upon which Goodnight (1940b) has founded a subfamily Branchiobdellinae. That this difference is a fundamental one has been established by the recent examination of a European species of the genus, which has revealed additional peculiarities of the reproductive system as well. All the North American genera which have been studied in detail have two pairs of testes, and thus belong to Goodnight's subfamily Cambarincolinae. With *Branchiobdella* still very poorly known taxonomically, it is premature to postulate which of these two conditions is a primitive one.

Funnels. Spermatozoa are collected from the coelomic spaces of the testicular segments by the modified ends of the efferent ducts, which assume the general shape of a laboratory thistle-tube funnel—a subglobose enlargement, a subterminal constriction, and a slightly flared free margin. The entire structure is composed of a single layer of densely ciliated epithelial cells, and apparently varies in size and to some extent in shape among different species and genera. Normally the funnels are located in the lower posterior portion of the segments, their openings directed dorsolaterad and easily detected by the densely aggregated spermatozoa. Owing to the difficulty of obtaining precise measurements from whole mounts, and the general similarity of the funnels throughout the genus *Cambarincola*, their possible taxonomic utility has not been carefully investigated.

Efferent ducts. Each funnel is attached to a slender tubular efferent duct, which proceeds ventromesad into the vicinity of the bursa in segment VI. Here it unites with that of the opposed funnel, forming the deferent duct. The efferent ducts serving the funnels of segment V penetrate the septum of segments V/VI near its ventral margin, mesad to the funnels. Those confined to segment VI are to be found in the ventral portion immediately caudad to the bursa.

Deferent ducts. These conduits, formed by the union of a pair of the smaller efferent ducts, are histologically similar to them but average considerably larger in diameter. Originating in the general region of the atrial portion of the bursa, the deferent ducts proceed

more or less directly dorsad to merge with the ental end of the spermiducal gland, either more or less abruptly, or by way of an attenuated lobe of the latter organ. Holt (1954) has remarked considerable difference in the diameter of the deferent ducts between *C. branchiophila* and *C. philadelphica*, suggesting that in sectioned material it may be possible to note size differences of taxonomic significance.

Spermiducal gland. The union of the two deferent ducts brings us to an abruptly larger and more intricate portion of the sperm transfer system. This is a rather plump and heavily glandular organ of very variable size, shape, and proportions, composed internally of a single layer of glandular epithelium. It is located in all species on one side of segment VI, lying in the coelomic cavity between the gut and body wall and readily visible in well-cleared whole mounts. In all species of *Cambarincola*, the spermiducal gland is oriented in a distinctly oblique plane across the segment, with the ental end cephaloventrad in location, and the ectal end caudodorsal. In contracted specimens the orientation may be dorsoventral; eversion of the bursa tends to draw the ectal end ventrad, bending the gland into a C shape or alining it horizontally.

The precise function of the spermiducal gland remains in some doubt, although from its histological character we can assume it contributes some material beneficial to the passage of spermatozoa or to the accomplishment of sperm transfer. Anatomically, it is to be considered a specialized section of the deferent ducts both prior to, and ectad of their commissure into a single conduit. In some genera, such as *Branchiobdella*, the deferent ducts enter into the gland quite near its ectal end, with the main bulk of the organ greatly prolonged entally and variously coiled in the coelom. In *Cambarincola* and its related genera, the gland is basically Y or T shaped, the ental branches forming the places of entry of the deferent ducts, and this arrangement, from a morphological standpoint, is probably a reflection of the primitive form in early branchiobdellids. Departure from this arrangement seems to occur chiefly in the genera which are concomitantly specialized in other respects as well; in the spermiducal gland we have, therefore, a useful sort of yardstick for gaging affinities.

Assuming that a Y-shaped gland is a generalized condition, we can likewise essay an arrangement of the species of *Cambarincola* into groups or series of progressive specialization, culminating with the gland taking a simple tubular form with little or no lobing at the entry of the deferent ducts so that the Y shape is essentially lost. This morphological progression is one frequently employed in the following classification of the genus. When the entry of the ducts is marked by an acuminate production of the gland, so that the transition is a gradual one, the gland is regarded as "lobed" and the

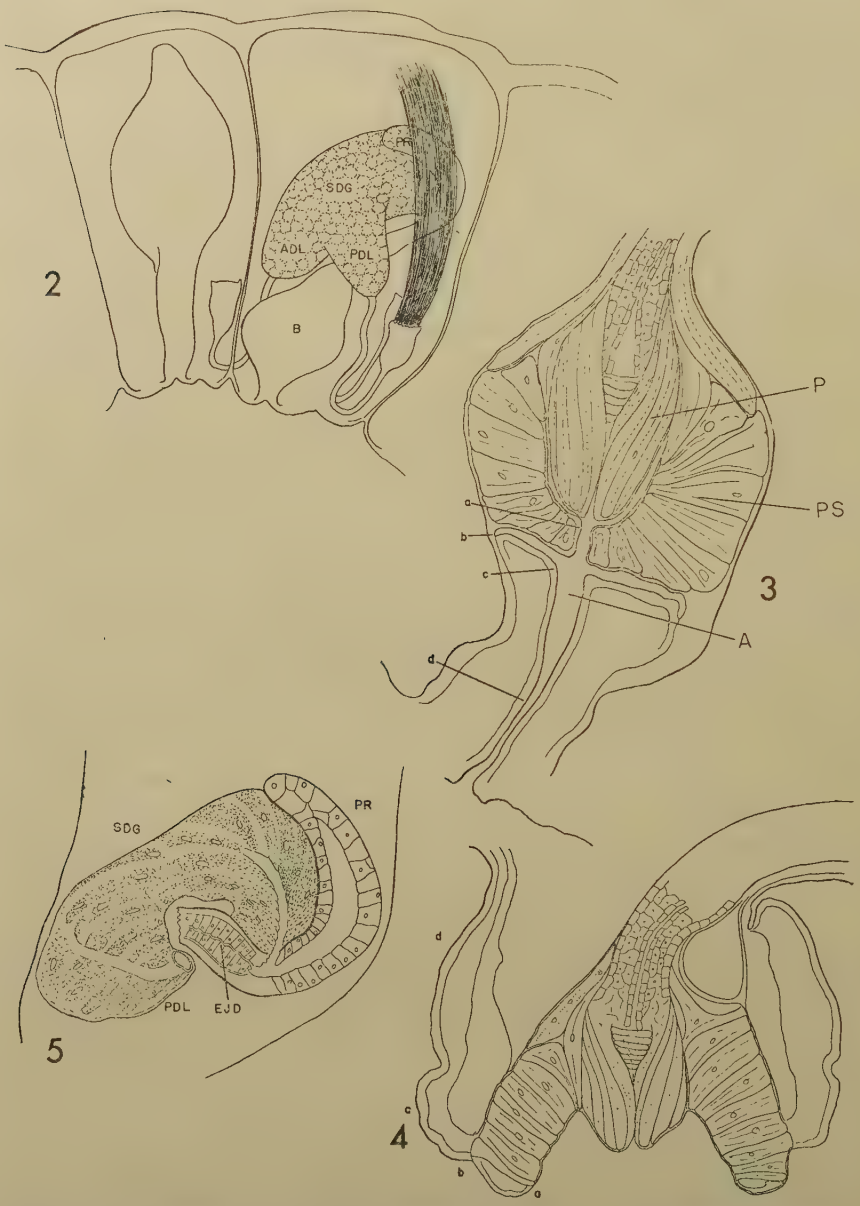
lobes are called anterior or posterior deferent lobes according to the position of the deferent ducts which enter them. The posterior ducts collect spermatozoa from the sixth segment, the anterior ducts from the fifth.

Prostate gland. This tubular structure is the "accessory sperm tube" of Ellis and other workers, but its function is almost certainly at least analogous to that of the prostate gland in other animal groups. Anatomically it originates at the junction (in most cases) of the spermiducal gland and the ejaculatory duct, and extends entally along the gland, both closely invested with a common (peritoneal) membrane. The histology of the prostate varies considerably. In some species it is superficially almost identical with the spermiducal gland in appearance, as regards both the size and apparent composition of the cells. In others there is a remarkable difference, one visible even under low power magnification, in that the prostate is made up of very large vacuolated cuboidal epithelial cells apparently with little or no secretory contents.

The actual size and shape of the prostate gland varies to a considerable extent, chiefly in diameter and length with respect to the spermiducal gland, and this variation is often of considerable diagnostic importance. It is of course necessary to make certain that the true dimensions are determined by a careful observation—the prostate is often partially concealed or its ental end turned away from the major axis, creating a much foreshortened effect. In at least one case, the diameter of the prostate in comparison with that of the spermiducal gland provides the major basis for separation of two species of the genus.

Entally the prostate ends blindly, although in the group in which it is histologically distinct from the spermiducal gland, there is a terminal development in the form of a clear bulb generally about the same diameter as the prostate proper, but occasionally somewhat rudimentary (in primitive species) or quite enlarged in specialized forms. The relationship of terminal bulb to vacuolated epithelial cells is so constant that the one is prima facie evidence of the other even when conditions prohibit direct observation of both!

Within the family Branchiobdellidae, the prostate gland apparently typifies the group of genera clustered around *Cambarincola* and may therefore serve a useful purpose as a tribal or subfamilial character. It is considered to be, in its simplest form, an outpocketing of the spermiducal gland which has, in the course of evolution, become histologically differentiated and altered in size and shape (from a broad short process to a long, slender, tubular one). I suspect that in at least one specialized branch of this part of the family, that which has produced *Ceratodrilus*, the tendency has been toward consolidation



FIGURES 2–5.—Cross-sections of male reproductive organs. 2, Reproductive systems of *Cambarincola shoshone*, showing typical orientation and location of the major organs within segments V and VI; 3, section through bursa of *C. ingens* in normal position; 4, cross-section through bursa of *C. ingens* in everted position; 5, cross-section through spermiducal gland, prostate, and part of ejaculatory duct in *C. philadelphica*. Histology semidiagrammatic, but size and shape of individual cells shown correctly. Abbreviations: A, atrium of bursa; ADD, anterior deferent duct; ADL, anterior deferent lobe

of the prostate back into the spermiducal gland, so that all remaining of it in existing species of that genus is the bulbar tip, occurring as a protuberance on the dorsal side of the gland near its ental end.

Ejaculatory duct. The spermiducal gland discharges to the outside through a tubular duct with distinctly muscular walls which is undoubtedly capable of spasmodic or peristaltic action, and which is appropriately named the ejaculatory duct (Holt, 1949). Both the structure and distribution of this duct vary greatly in the family. In certain genera (e.g., *Xironogiton*), it is quite thin-walled, probably the primitive condition. In at least one undescribed species referable to *Xironodrilus* in the sense of Ellis, it is absent altogether. In *Cambarincola macbaini* (for which a new genus is being proposed elsewhere), it is greatly enlarged and filled with a mass of convoluted tubing. From the morphological standpoint, the duct is simply a segment of the main sperm conducting passage; we should therefore expect the least modified condition to reflect the generalized or primitive state. Insofar as *Cambarincola* in the strict sense is concerned, the ejaculatory duct is basically similar through all the species—of about the same proportionate length and with a moderately muscular wall. Ectally it merges gradually into the penial sheath of the bursa.

Bursa. This, the outermost differentiated portion of the male reproductive system, is fundamentally a muscular invagination of the ventral body wall—invaginated to permit concealment of the penis well within the body, and muscular to achieve extrusion of the penis during copulation. The accompanying illustrations (figs. 3 and 4) afford some idea of the composition of the bursa, which is divided into two major anatomical parts: the penial sheath and the atrium.

In virtually all branchiobdellids the bursa is a subglobose to pyriform organ opening to the exterior at the midventral part of segment VI. Typically it projects mesad into the coelom or is directed somewhat caudad. Its ental half is taken up largely by the penial sheath (fig. 3, PS) which is the somewhat differentiated muscular area surrounding the ectal end of the ejaculatory duct and the virtually continuous penis. The latter is very variable in structure through the family, taking the form of a simple truncate cone which terminates the ejaculatory duct, or becoming gradually modified into a much

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of the spermiducal gland; B, bursa; EB, ental bulb; ED, ectal duct; EJD, ejaculatory duct; EP, ental process; P, penial part of bursa; PDD, posterior deferent duct; PDL, posterior deferent lobe of the spermiducal gland; PR, prostate gland; PS, penial sheath of bursa; SDG, spermiducal gland. The lower case letters a–d in figures 3 and 4 are located at the same anatomical position in both drawings.

longer structure capable of being itself everted independently of the bursa. The evolutionary trend in this particular is obvious enough.

In *Cambarincola*, the penis is invariably of the short cone type, and does not, in repose, extend ectad beyond the major band of circular muscle which approximately divides the bursa into halves. During copulation it is carried to the exterior by eversion of the bursa, which thrusts the penis and associated penial sheath down through the atrium and to the position it occupies as a median projection in a circular, distally concave structure formed by the lining of the atrium. This displacement of the atrium during eversion can be appreciated by comparison of the guide letters *a* through *d* in figures 3 and 4, showing that the inner wall of the atrium becomes the outer surface of the everted bursa. As the penis is, in this genus, capable of only limited penetration of the spermatheca of the copulatory partner, it is evident that the animals are obliged to achieve and maintain a very close ventral contact during the process of sperm transfer.

Eversion of the bursa is accomplished partly by contraction of the circular muscles of the ental half, and doubtless also in part by internal pressure achieved by contraction of the segmental muscles.

Summary of the male sex organs. Holt (1949) has shown that the entire male system, with the exception of the funnels and possibly the efferent ducts, is ensheathed by peritoneum, and all of the organs so invested are probably derived from the body wall. The interested student is referred to this paper for a more detailed treatment of the reproductive system. For the present, I consider them chiefly from the standpoint of their taxonomic utility.

It is postulated that the primitive arrangement for the family consists of two pairs of testes, funnels, and efferent ducts, one pair each in segments v and vi; two deferent ducts which merge into a Y-shaped glandular enlargement, the spermiducal gland—which probably lacks a prostate, and which does not extend entally beyond the entry of the deferent ducts; a thin-walled, muscular ejaculatory duct, and a simple, fusiform, eversible bursa which carries a short, conical, unmodified penis in its ental half.

Except for the presence of a prostate, the animal which comes closest to answering this description is a species of *Cambarincola*, to be described in a following section. Species which are almost antithetical to the foregoing are likewise known, but are members of North American genera as yet undescribed. However, a general progression away from most of the stipulated conditions can be found within the confines of the genus *Cambarincola*, suggesting its status as a dynamically evolving genus which has nonetheless retained, in

a relict status, species which approximate the postulated form of the ancestral stock.

VI. Female Reproductive System

The female sex organs are much less intricate than those of the male system, and are of considerably less significance in arriving at groupings of species. Perhaps of greatest utility is the general form of the spermatheca in providing supplementary points of difference between related forms.

Ovaries. The ovaries of branchiobdellids are located in the coelom of segment VII, and offer little for systematic use. The relative amount of their development, of course, provides a measure of the maturity of a specimen. In some species of the family, segment VII is rather distinctly the largest of the body units, and may enlarge anteriorly to somewhat overlap on the posterior part of segment VI. Insofar as *Cambarincola* is concerned, however, no appreciable differences are apparent either in the ovaries or the segment in which they occur.

Spermatheca. The spermatheca, throughout the family, so far as known, is a tubular structure formed by invagination of the mid-ventral body wall of segment V, and of variable size and shape. It is composed of several anatomically and histologically distinctive sections reflecting different aspects of the function of sperm reception, storage, and discharge. In some genera, of which most are still undescribed, the ectalmost part of the spermatheca is an enlarged, muscular structure reminiscent of the bursa, and possibly discharging a similar function. In *Pterodrilus* and *Cambarincola*, at least, the spermatheca begins ectally with a thin-walled, muscular duct which proceeds dorsolaterad around one side of the gut, terminating in a variously enlarged, fusiform to globose reservoir or ental bulb, the function of which is storage of spermatozoa. Histologically this part of the spermatheca differs appreciably from the duct in being only slightly muscular, and in gross appearance it is frequently semi-transparent or clear-walled. The diameter of this portion is subject to much variation, depending largely on whether or not it happens to contain sperm masses; however, the ratio of its length to that of the ectal duct seems to be relatively constant, and thus is available for diagnostic use. In various members of the genus, the ental bulb is terminated by an abruptly smaller lobe or process, the ental process. This is composed of deeply staining, small epithelial cells containing much granular material. These cells are doubtless secretory in function. As the ental process appears in general to be present and best developed in specialized members of the genus, it may be provisionally considered an evolutionary improvement in the spermathecal struc-

ture. Perhaps it provides some sort of secretion which facilitates longer retention of viable sperm. Generally speaking, in species which have been adjudged conservative or primitive on the basis of other characters, the spermatheca tends to have a long, slender ectal duct and a small, globose ental bulb without an ental process. More specialized species reduce the length of the ectal duct, enlarge the ental bulb, and add a glandular ental process.

Relationships Within the Family

So far, not enough is known of the branchiobdellids to permit the formulation of any lasting concepts about the affinities of genera to each other. A major difficulty lies in the fact that heretofore the classification has been based on characters which probably are of little phylogenetic significance, and preexisting genera have been heterogeneous as well as very poorly known. With the establishment of some comparatively severe generic definitions (only comparable, however, to those used in other phases of systematic zoology), it seems possible to summarize general impressions and ideas accumulated during this study of *Cambarincola*.

Although the Branchiobdellidae is a normally homogeneous family as regards general organization of body form and organ systems, histology, and way of life, a very considerable variation affects the structure of the reproductive systems. A basic dichotomy was made by Goodnight (1940) in recognizing two subfamilies according to the distribution of male germinal tissue. For species in which testes, or the morulae which they produce, occur only in segment VI, Goodnight proposed a subfamily Branchiobdellinae; for those in which spermatozoa are produced in segment V as well as VI, he provided the name Cambarincolinae. This difference, of course, had already been used by Pierantoni (1912) as a generic character, and does appear to be a fundamental distinction, particularly as it is reinforced, at least in the one species of *Branchiobdella* which I have examined, by correspondingly important differences in organization of the larger and more ectal parts of the male reproductive system.

Another basically important anatomical distinction between genera emphasized by several workers is the nature of the outlet of the anterior nephridia. In some genera the two ducts open to the outside independently of each other; in others there is a commonly shared nephridiopore. However, the nature of this relationship is often (in fact usually) difficult to detect with complete confidence, and we are denied the use of literature reports based on the study of whole mounts. In cases where the nephridiopore has been carefully studied by the use of serial sections, it does afford strong presumptive evidence of relationships.

The basic similarities in structure, shape, arrangement, and histology of the reproductive systems, however, certainly represent the best reflection of affinities. That this statement is true within the confines of genera is strongly supported by the findings outlined in the systematic treatment which follows. The thin, and usually subjectively drawn, line between species groups and genera permits, I think, an extension of the principle into so-called higher categories.

From the preceding discussions of characters, it will be recalled that within the limits of *Cambarincola* one finds a fair amount of variation within the reproductive system both in the gross and histological appearance of the individual organs. The casual observer might suspect, perhaps with justification, that by placing major emphasis upon different organs one could arrive at several entirely different classifications. This is not only theoretically true, it is a difficulty which has been a source of vexation since this investigation was begun. The solution has been an arbitrary one, influenced in no small measure by the more or less unconscious accumulation of small impressions which collectively result in a conscious allocation of species by the totality of their characters. After several abortive classifications had been drawn up and found wanting, I struck upon the one which immediately appeared satisfactory and this, which has met the test of having to accommodate additional and unforeseen species, is the one here used. The organization of the bursa is given pre-eminence, within limits, in the definition of the genus.

In the preceding section I have discussed something of the variability of this structure among various branchiobdellids, and pointed out that a surprising amount of diversification is to be found in such a basically simple arrangement. There is now known to be a number of species which share the fundamental "cambarincoloid" organization of bursa, ejaculatory duct, spermiducal gland, prostate gland, two deferent ducts, and four efferent ducts and funnels, in addition to a terete body form and a generally similar appearance. However, a detailed study of the bursa shows that on the basis of its several modifications, these species can be classified into groups, in which the component species are obviously quite similar and related in small details as well as overall facies. That bursa structure is a character of major importance is attested by the homogeneity of these groups, which are certainly entitled to be called genera by any definition but the most inclusive. It is now altogether likely that "Cambarincola" in the usage of Ellis will be found to correspond roughly to the bounds of a subfamily[!] in terms of modern classification.

We have, then, to consider basically a number of species of North American branchiobdellids in which the body is cylindrical, the nephridiopore single, the spermatheca not divided or branched,

segments v and vi testicular, and the male sex organs consist of the elements listed in the preceding paragraph. Discounting poorly described species, there are about 18 forms, which Goodnight placed in the 3 genera *Pterodrilus*, *Cirrodrilus*, and *Cambarincola*. Of these three, *Cirrodrilus* has been disposed of (Holt, 1960a) in a careful paper which restores the correct name *Ceratodrilus* to the American species and elucidates the anatomy of the genus. This genus differs from all others in the collective characters of (1) eversible penis, (2) virtual absence of the prostate gland, (3) great elaboration of segmental and peristomial epidermal tentacles.

Cambarincola in the usage of Ellis and Goodnight is of course heterogeneous. The genus in the strict sense includes only those species which do not have segmental ornamentation, in which the bursa, but not the small penis, is eversible (or extrusible), the ejaculatory duct is not strongly modified, and the prostate gland is present and functional. This combination of characters rules out three known species originally described in the genus: *inversa* Ellis, *elevata* Goodnight, and *macbaini* Holt. Each of the last two named represents a distinct generic type, now being defined and readied for publication by Professor Holt. We have studied the types of *C. inversa* and regard it, too, as worthy of generic rank, but action is deferred pending the acquisition of fresh material for sectioning.

Pterodrilus is likewise heterogeneous. The species *alcicornus* and *distichus* (with two additional undescribed forms) are basically very similar internally. *P. mexicanus* is still unknown save from the poorly preserved type specimen. But *P. durbini* of Ellis is remarkably different, and belongs to the recently described genus *Ellisodrilus* (Holt, 1960b), along with a second, previously unknown related species, *E. clitellatus*.

With all of these eliminations and realinements which have resulted from a close comparative study of important internal organs, we are left with a genus *Cambarincola* in a strict sense (which nonetheless is now known to contain no less than 21 species), and a genus *Pterodrilus* with two known and two more undescribed forms; and insofar as internal structure is concerned, these two genera might be considered identical.

Here the element of arbitrary decision has its hour upon the stage. Some authors who may work with branchiobdellids at a future time will perhaps desire to combine the two genera under the older name *Pterodrilus*. My personal feeling is that although the two groups are beyond peradventure very closely related, the evidence suggests that the species of *Pterodrilus* represent an extreme specialization of some early embranchment of the Philadelphica section of *Cambarincola*. Evolutionary recency is suggested by the small size of the

species, greatly reduced jaws, moderate to elaborate development of segmental ornamentation, and extreme enlargement of the prostate both with respect to its size in comparison with the spermiducal gland, and as regards the great size of the individual cuboidal cells.

Critics of a narrowly defined genus might object that *Pterodrilus* differs less from the Philadelphica section of *Cambarincola* than the latter does from the Mesochorea section. But this is a matter of personal preference, and something which must be settled by the test of future usage. The recognition as a genus of a specialized offshoot of some diverse genus has ample historical precedent. The lizard genus *Uta* is generally recognized as only a modification of one of the groups of *Sceloporus*, and doubtless a long list of similar evidence could be marshalled in support of the *Pterodrilus-Cambarincola* relationship.

Unfortunately, as regards other genera, relationships are not so clear. The tendency toward development of an eversible (and ultimately an extrusible) penis seems clearly a specialization, but one which had perhaps been achieved independently and at different times. Within the group of genera which are so endowed, there exists considerable variation as regards presence or absence of the prostate, modification of the ejaculatory duct, and modification of the spermatheca. Since these genera are composed largely of very small worms, with every indication that a great many remain to be found and studied, it would be premature to venture any opinion on their affinities.

Whether the genera *Triannulata* and *Stephanodrilus* (the latter in the sense of Goodnight's usage of it for a Californian species) differ from *Cambarincola* is something which remains for future settlement.

Phylogenetic Considerations

The following remarks constitute an attempt to summarize the inferences which can be reasonably drawn from our present state of knowledge of the genus *Cambarincola*. It seems relatively safe to assume that probably most of the more common species of the genus have been described, although a number of localized forms undoubtedly remain to be discovered.

Some criteria have been set up for the evaluation of certain diagnostic characters against the standard of a hypothetical ancestral condition (cf. pp. 281–291). On the basis of these criteria, it is possible to consider some species as primitive and some as specialized in the two largest sections of the genus. By restricting comparisons to the members of a given section, rather than the genus as a whole, we find that the presumptive conservative forms tend to be scarce,

localized, and on or near the periphery of the range of the group or section.

Most of the United States, east of the 105th Meridian, is occupied by at least two species of *Cambarincola*, although as a rule the area shared by any two given species is not extensive (*mesochorea* and *vitrea* have the greatest territory in common). The number of species tends to increase in certain regions—to five in the Ozark area and to seven in southwest Virginia (the Pacific Northwest, still largely unknown, must be omitted from consideration but it probably also has a large number of species).

Now the interesting inference to be drawn from known distributions in the genus is that—in comparison with other members of their respective subgeneric section—none of the species of the Appalachian fauna can be considered as primitive, such forms rather occurring in lowland regions where two or three widespread forms of *Cambarincola* are the dominant and often the only branchiobdellids. In short, morphologically primitive species do not occur in the regions having the richest branchiobdellid fauna at the present time.

It will be recalled from a previous section (p. 290), that the generalized species of *Cambarincola* represent to a considerable extent the hypothetical form and structure of the familial archetype, and that members of the Mesochorea section of the genus lack specializations in virtually all of the major diagnostic characters. It is therefore particularly significant that these species are, in a sense, now known largely as relicts strung out along a highly probable route of migration taken by cambarine crayfish in their occupation of eastern North America. The two most primitive known species of the genus are endemic to the Ozark region. A single species (*holti*) of the Macrocephala group occurs in central Kentucky; its nearest relative in the Columbia River system. The two species of the Branchiophila group have essentially the same sort of transcontinental distribution.

The distinctly more specialized Philadelphica group has its center of abundance in the southern Appalachians where six species occur, along with a variety of species of *Pterodrilus* and *Xironodrilus*. One species of the Philadelphica group, *macrodonta*, occurs in the foothills of the Rockies and in the adjacent High Plains, but it may be continuously linked up with the Appalachian fauna by way of Wisconsin and Michigan (see map, fig. 57). Another species, *chirocephala*, extends westward into the Ozarks and adjacent Great Plains. Two other closely related species, *osceola* and *vitrea*, occur in the Great Plains and southeastern Coastal Plain; they are both somewhat primitive within the Philadelphica section. The true Appalachian endemics (*C. ingens*, *C. heterognatha*, *C. holostoma*, and *C. fallax*, all of the Philadelphica group, and the one known species of the Demissa

section) are all specialized both in their respective sections as well as in the entire genus.

It is, unfortunately, not possible to date the course of events in a postulated phylogenetic scheme in any but the roughest terms. We can assume from paleobotanical evidence a widespread occurrence of the so-called Arcto-Tertiary forest across midland North America as late as the Miocene, and the gradual conversion of this area into semiarid grassland in the Pliocene. This change of basic habitat must have commenced a schism of earlier broad ranges which was culminated by Pleistocene glaciation.

The apparent lack of endemism in glaciated parts of the continent suggest both a low rate of evolution and relative recency of postglacial northward migration by crayfish. The presence of *C. philadelphica* in Wisconsin is in all probability due to its isolation there in the well-known driftless area. At present I know of no authentic records for the species between Wisconsin and New York.

A very provisional reconstruction of the events by which *Cambarincola* has undergone dispersal and evolution in North America might be about as follows:

1. The procambarincolid stock arrived on this continent from northeastern Asia, as commensals on primitive astacine crayfish perhaps during late Cretaceous or early Tertiary times. During this period western North America was subjected to considerable uplift and downwarping; large extensions of the sea covered much of the southwest and it seems doubtful that crayfish were able to occupy much territory until the Eocene brought widespread emergence and generally uniform subtropical climate to the continent. The spread of the cambarine crayfish (which presumably evolved in America by the loss of branchial elements and specialization of certain pleopods) into eastern North America could scarcely have taken place prior to withdrawal of the midcontinental Cretaceous embayments.

2. The species of the Mesochorea section of the genus developed in something like their present form, with numerous species or widely ranging ones (perhaps both) similar to the Recent *C. ouachita,* occurring nearly across the continent.

3. Perhaps along with the crayfish genera *Orconectes* and *Cambarus,* cambarincolids occupied the Appalachian system, which was then being developed by dissection of the old Cretaceous peneplain and doubtless afforded a new type of habitat. Here both crustaceans and annelids prospered, and the Philadelphica section had its origin by gradual differentiation of the prostate gland and diminution of the deferent lobes of the spermiducal gland. New and more specialized forms continued to evolve here, doubtlessly enhanced by the opportunities for localized geographic speciation in mountainous terrain,

causing older forms of the section to become extinct or isolated in less competitive situations (such as the semilowland habitat occupied by *C. virginica*).

4. The preceding events probably occurred prior to and during the Miocene. We can postulate that two major groups of species existed: a primitive group of species in the midcontinental region and a specialized, more rapidly evolving one in the still rugged Appalachians. In late Miocene, however, the moderation of earlier climate brought a change to North America, replacing the subtropical plant life with a more boreal Arcto-Tertiary flora and inaugurating more pronounced seasonal cycles. This now widespread environment may have favored the expansion of specialized cool-water forms westward into the range of older species and must have caused a decline in the abundance of the latter. Possibly the *philadelphica* stock spread as far west as Colorado at this time.

5. During the Pliocene abrupt climatic changes occurred, owing to considerable orogeny in the Pacific Coast region and elsewhere, converting the Interior of the continent into a subarid grassland and creating extensive desert areas in the intermontane basins. The distribution of *Cambarincola* was at this time severely fractured, with the Mesochorea section remaining as a rather relict group on both sides of the Continental Divide. The Philadelphica section, which had spread westward only as far as the present site of the Rockies, was thus contained in eastern North America.

6. The effects of Pleistocene glaciation on *Cambarincola* have probably been only to pre-empt species from higher latitudes in eastern North America. Only fairly widespread and successful species have invaded glaciated terrain. No new species of this genus seem to have evolved during this process. *Pterodrilus distichus* Moore is known to be virtually restricted to glaciated areas, and three or four species in more highly specialized genera, as yet undescribed, are either endemic to glaciated areas or are most abundant there. Whether this reflects accelerated evolutionary rates or greater adaptability in the occupation of new terrain than in *Cambarincola* I cannot guess.

It is finally interesting to observe that utilization of crayfish as habitat by branchiobdellids must antedate the evolution of the American cambarine crayfish, since several congeneric species in at least three branchiobdellid genera inhabit both *Pacifastacus* of the Astacinae and various genera of the Cambarinae. Without direct geological evidence, we can safely grant the genus *Cambarincola* a considerable antiquity.

Systematic Treatment

Genus *Cambarincola* Ellis

Cambarincola Ellis, 1912, Proc. U.S. Nat. Mus., vol. 42, p. 481; 1919, vol. 48, p. 190.—Goodnight, 1940, Illinois Biol. Monogr., vol. 17, No. 3, p. 30.—Holt and Hoffman, 1959, Journ. Tennessee Acad. Sci., vol. 34, p. 102.

TYPE SPECIES.—*Cambarincola macrodonta* Ellis, 1912, by original designation.

DIAGNOSIS.—Branchiobdellidae with the following characteristics: Body terete, without specialized projections; jaws normally large and massive, subtriangular in dorsal aspect, the dorsal jaws with a large median tooth and usually two smaller cusps on each side (these subequal to median tooth in one form), the ventral jaws with normally a median sinus and two large paramedian dentations, or occasionally of the same form as the dorsal. Anterior nephridia opening through a common median dorsal papilla on segment III.

Male reproductive system. Bursa subpyriform to obcordate, becoming broadest entally, capable of being everted; ental portion of bursa modified into a penial sheath enclosing a distinct, subconical penis which is noneversible but is carried to the outside by eversion of the entire bursa. An ejaculatory duct is present, normally at least half as long as the bursa and with strong muscular walls but not otherwise enlarged or specialized; spermiducal gland relatively large, basically cylindrical but occasionally compressed and/or produced into a large subterminal lobe at the entry of one of the deferent ducts, histologically the gland is composed of tall, columnar, basophilic glandular cells surrounding a rather narrow lumen. A prostate gland is present, its origin adjacent to the commissure of the ejaculatory duct and spermiducal gland; length and diameter variable but normally of much smaller dimension than the spermiducal gland against which it is closely applied (the two structures are enclosed by a common membranous sheath). Histologically the prostate may be similar to the spermiducal gland or may be composed of large, vacuolated cuboidal epithelial cells which contrast strongly with the smaller glandular cells of the gland itself, in this condition the prostate always terminates entally in a thin-walled bulbous structure.

Female reproductive system. Spermatheca with a more or less elongate ectal portion, generally distinctly muscular, and a thin-walled ental portion normally expanded or enlarged and capable of much distention, often with a smaller ental process. Spermatheca never branched or diverticulate.

DISTRIBUTION.—So far as is known, *Cambarincola* is endemic to North America. The majority of the known species occur in eastern United States, although several have been found in the Columbia

River system, and it is to be expected that further explorations will greatly augment the list of forms inhabiting northwestern North America.

Endemism apparently is characteristic of several species on a very localized basis. Most of the species are known from a number of localities even though the totality of the specific range may be very modest; but several forms are still known only from their type localities. In a general way, it appears that species of moderate size enjoy the widest distributions, with both very large and very small species being more or less limited to relatively small confines—usually in mountainous regions.

Goodnight (1939), on the basis of the 21 species of the family which he knew from North America, established four major faunal assemblages (he called them "faunal regions") characterized by various groups of species and genera. Now although the recognition of faunal assemblages associated with different physiographic regions is a natural and very desirable outgrowth of systematic studies, it must be obvious to the most naive that such arrangements are no better than the current state of taxonomic knowledge. Goodnight's proposal was made 20 years too soon, at the very least, since he knew but a fraction of the actual number of American species of Branchiobdellidae.

Subgeneric groupings.—Generally any large ensemble of species of a given genus will be divisible into groups of related forms, although the actual degree of affinity may be quite variable. Since an understanding of phylogeny and evolution depends largely upon the arrangement of species into progressively smaller ranks with progressively greater interspecific similarity, I have endeavored to allocate the species of *Cambarincola* which I have personally studied into a subgeneric classification. This system is above all a subjective one, both in the selection of diagnostic characters and the relative importance assigned to each. That it will be immune to future modifications, or even abolition, now seems improbable. I suggest a basic division into three sections, two of which are large and diverse enough for further refinement into groups. In one case, subgroups are introduced.

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It must be emphasized that although clear-cut distinctions are made in keys and diagnoses, there appear to be no major breaks anywhere in the genus, either in a single structure or group of characters in combination, that might conceivably threaten the homogeneity of *Cambarincola* as a generic entity.

Key to Sections of the Genus *Cambarincola*

1. Prostate and spermiducal glands of the male reproductive system histologically similar, both containing visible secretory granules 2
   Prostate and spermiducal glands dissimilar in histological appearance, cells of the former lacking visible secretory granules.
   PHILADELPHICA SECTION (p. 320)
2. Prostate gland terminating in a small clear bulb; all of the reproductive organs drastically reduced in size . . . . . DEMISSA SECTION (p. 365)
   Prostate gland not terminating in a clear bulbar structure; reproductive organs all of normal size for the genus . . . MESOCHOREA SECTION (p. 301)

MESOCHOREA SECTION

Six species of the genus are here referred to the section typified by *Cambarincola mesochorea*, in which the prostate gland is histologically similar to the spermiducal gland, and the latter is normally provided with large and distinct deferent lobes. These species are further

segregated into three groups based upon more numerous similarities in details of both body form and reproductive organs.

Presumably this section includes the more primitive species, or at least those in which presumed primitive characters are preserved. With one exception, each species is remarkably localized, four being known only from the type localities, the fifth from only two places. I should expect that such distributional patterns would be indicative of reliction, following disintegration of a formerly more inclusive range of the parental stock. The localized species now occupy peripheral localities on the known distribution of the section; *C. mesochorea* alone is widely distributed in the central area. That it is possibly the most specialized of the six correlates well with its present abundance and extensive geographic range.

Key to Groups of the Mesochorea Section

1. Prostate gland appreciably broader and longer, in most specimens, than the spermiducal gland; latter essentially without distinct lateral deferent lobe. MESOCHOREA GROUP (p. 302)

   Prostate gland equal in size to, or much smaller than, the spermiducal gland; latter with either subequal terminally located deferent lobes (thus T- or Y-shaped) or with a distinct lateral lobe 2

2. Spermiducal gland long and cylindrical, terminating in virtually similar deferent lobes; prostate fully as long as spermiducal gland. Very large species, with tentaculate peristomium . . MACROCEPHALA GROUP (p. 311)

   Spermiducal gland shorter, cuneate or acuminate, terminating in a major deferent lobe subtended by a smaller lateral lobe (sometimes these may appear terminal and subequal); prostate gland only half as long as spermiducal gland or less. Small species, the peristomium not tentaculate. BRANCHIOPHILA GROUP (p. 316)

MESOCHOREA GROUP

Proposed for the inclusion of three rather generalized or primitive species, this group is to be ranked at the bottom of the evolutionary scale in the genus, although its components show considerable differentiation among themselves. Similar in general form of the male sex organs to the species of the Macrocephala group, the present species lack any of the specializations which mark the others. The prostate is greatly enlarged and the posterior deferent lobe is virtually obliterated in two species although still conspicuous in the other.

Cambarincola mesochorea is fairly widespread over the interior of the continent; *C. ouachita* is known only from the type locality in southeastern Kansas. This is a most unusual relationship and one warranting further study. The two species are very similar in their medium size, general body outline, jaw structure, and reproductive systems. *C. restans* is remarkably different from anything else in the genus because of its head size and body shape. The sex organs are much

like those of *mesochorea*. I would arrange these species in the following order of advancement: *ouachita*, *restans*, and *mesochorea*, although this is a merely relative sequence and does not imply a straight line of descent. Despite its several distinctive characters, *mesochorea* has been confused with both *C. macrodonta* and *C. vitrea* in earlier literature; it is probably the basis for many of Goodnight's records for both *macrodonta* and *philadelphica*.

Key to Species of the Mesochorea Group

1. Spermiducal gland with a large, conspicuous, posterior deferent lobe at its midlength; body form somewhat xironodriloid (southeastern Kansas).
Cambarincola ouachita, new species
Spermiducal gland without a large median posterior deferent lobe, the deferent ducts entering the extreme ental end of the gland with no enlargement; body form distinctly cambarincoloid 2
2. Body form normal for the genus, head smaller than the second body segment, body diameter increasing up to segment VI or VII (entire Mississippi River system) . . . . . **Cambarincola mesochorea,** new species
Body form unusual: head half again as thick as largest body segment and as long as first five segments combined; all body segments of essentially the same diameter (northeastern Arkansas).
Cambarincola restans, new species

Cambarincola ouachita, new species

FIGURES 8, 9

TYPE SPECIMENS.—Holotype and one paratype, USNM 29937, from *Orconectes* sp., collected 4.3 miles west of the Montgomery County line on Kansas Hy. 168, Chautauqua County, Kansas by P.C. Holt, July 8, 1958.

DIAGNOSIS.—A rather large member of the Mesochorea group, differing from the other two by its larger, somewhat xironodriloid body form, and also by the presence of a large and conspicuous posterior deferent lobe on the spermiducal gland.

DESCRIPTION.—A medium-sized member of the genus, with a maximum length about 4.0 mm., the body rather elongated and parallel-sided (in both specimens), somewhat reminiscent of the shape of certain species of *Xironodrilus*. Segments II-VIII of about the same diameter and length; caudal sucker about as wide as head or segment I. Segments only a little longer than broad; prosomites not elevated over level of metasomites and less than twice the length of the latter.

Head of average size and form for the genus, as broad as segment I, not quite as long as first three body segments, the peristomium set off by a deep constriction and flared, but with entire margin.

Jaws robust, anisomorphic, dental formula 5–4, teeth subhomodont, acute.

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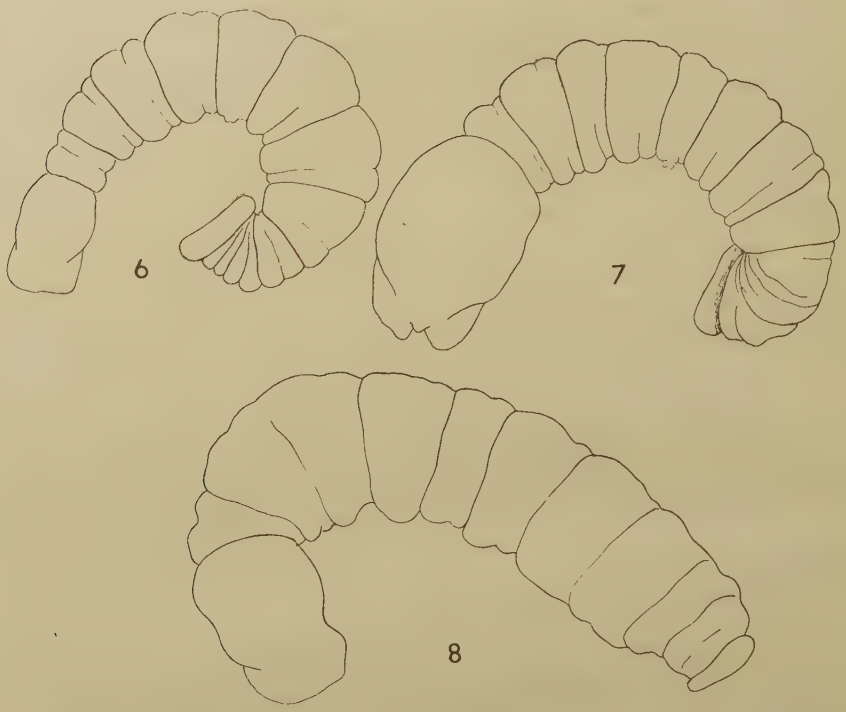


FIGURES 6–8.—Habit sketches of three species of the Mesochorea section, lateral aspect. 6, *Cambarincola mesochorea*, new species, paratype, Perry Co., Indiana (a little smaller than the normal adult size). 7, *C. restans*, new species, paratype from Benton Co., Arkansas. 8, *C. ouachita*, new species, holotype, Chautauqua Co., Kansas (specimen distorted in preservation). All figures drawn to same scale.

Male reproductive system occupying most of one side of the coelom of segment VI. Bursa elongate-fusiform, much longer than broad. Ejaculatory duct in type specimen recurved first ventrad then abruptly dorsad, drawing down the caudal end of the spermiducal gland. Latter elongate, cylindrical, curving cephalad across top of bursa, then ventrad to level of the middle of latter, thence mesad and tapering into the anterior deferent duct. Posterior deferent lobe very large and conspicuous, located at about midlength of spermiducal gland, directed caudad over base of ejaculatory duct and apex of penial sheath, thence caudomesad to merge with the posterior deferent duct. Prostate as large in diameter as spermiducal gland, curving along its dorsal side as far as the beginning of the anterior deferent lobe.

Spermatheca not completely visible in either type specimen, but appearing to be composed of a slender ectal duct and a subglobose ental bulb, no ental process observed.

Affinities.—In general body form, jaw structure, and great size of the prostate, this species is obviously allied to *mesochorea*, with which it is apparently sympatric. The major difference between the two lies in the large and distinct posterior deferent lobe of *ouachita*, and by the fact that the anterior lobe is somewhat longer than the prostate. Whether we are dealing here with two distinct species, or the local recrudescence of a primitive character within a population of *mesochorea* is something to be settled by future study of the Kansas-Oklahoma branchiobdellid fauna.

Cambarincola restans, new species

Figures 7, 10

Type specimens.—Holotype and two paratypes, USNM 29938, from *Orconectes* sp. taken in Sugar Creek, 2 miles north of Avoca, Benton County, Arkansas by P. C. Holt, July 6, 1958. Topoparatypes, PCH 768.

Diagnosis.—A species of the Mesochorea group, distinguished not only from its close relatives but from all other species of the genus by the accentuated head size and small body.

Description.—A moderately large worm, maximum length about 3.5 mm., the body form unusual in not being appreciably enlarged near the midlength, but of essentially the same diameter throughout, the caudal sucker a little larger in diameter than the preceding few segments. Prosomites about twice as long as metasomites, but the two subsegments of about the same diameter.

Head enormously developed, about as long as the first five segments combined and half again as broad as the greatest body diameter. Peristomium rather small, less than a third of the total head length, and not flared, divided into dorsal and ventral halves with a small lobe at the lateral sinus on each side but the peristomial margin not lobed. Head broadest at its midlength, tapering slightly toward the ends, the diameter about 75 percent of the length.

Jaws anisomorphic, subhomodont, the dental formula 5–4; the lateral cusps not appreciably smaller than the dorsal median and ventral paramedian teeth.

Male reproductive system similar to that of *mesochorea* in most respects, but the prostate not noticeably longer than the spermiducal gland, both somewhat arched in the coelom with the ectal end of the latter drawn ventrad by the ejaculatory duct (perhaps also by the pressure of the rather short segment). Prostate a little greater in diameter than spermiducal gland, its size increasing a little entally, terminating in a bluntly clavate lobe. Ental end of spermiducal gland T shaped, both deferent ducts entering at about the same angle, into very weakly developed deferent lobes. Exact shape of bursa not

FIGURES 9–12.—Reproductive systems of three species of the Mesochorea section. 9, *Cambarincola ouachita*, new species, holotype, Chautauqua Co., Kansas. 10, *C. restans*, new species, holotype, Benton Co., Arkansas (spermiducal gland mostly concealed by the large prostate). 11, *C. mesochorea*, paratype, Perry Co., Indiana (ental end of spermiducal gland curved mesad and not visible in this aspect). 12, *C. mesochorea*, new species, specimens from Kinney Co., Texas, outline in dorsal aspect to show complete length of prostate gland.

clearly shown in any of the specimens, but apparently much like that of the other species, in this case nearly twice the diameter of the spermiducal gland; penial sheath moderately small and confined to the ental third of the bursa as usual.

Spermatheca very large and robust, consisting of a short, very broad, muscular ectal duct and an ovoid, expanded ental bulb, both of these parts much broader in relation to the size of segment v than in any other member of the genus. No glandular ental process observed.

VARIATION.—No appreciable variation in size or proportions was noted in the type series, all from a single collection.

AFFINITIES.—This species is clearly a member of the Mesochorea group, and closely related to both of the other two forms, but like *mesochorea* particularly in the shape and relative size of the prostate

and spermiducal gland. In this respect it represents an advancement over the strongly lobed gland of *ouachita*.

Distribution.—Known only from the type locality. Presumably the species will be found to have a sporadic local distribution in the adjoining parts of Arkansas and Missouri.

Remarks.—The name *restans* is from the Latin; its meaning "left behind, exiled" seems particularly appropriate for the denomination of this odd, archaic creature.

Cambarincola mesochorea, new species

Figures 6, 11, 12, 13

?*Branchiobdella americana* Pierantoni, 1912, Ann. Mus. Zool. Univ. Napoli, new ser., vol. 3, No. 24, p. 17.

Cambarincola vitrea (in part) Ellis, 1919, Proc. U.S. Nat. Mus., vol. 55, pp. 257, 258 (Douglas Lake, Michigan, record).

Cambarincola macrodonta (in part) Ellis, 1919, Proc. U.S. Nat. Mus., vol. 55, p. 257 (Morgan City, Louisiana, record).

Type specimens.—Holotype and four paratypes, USNM 29939, from *Orconectes* sp. collected in a small gravelly stream 1.5 miles east of Adyville, Perry County, Indiana, by P. C. Holt, July 28, 1958. Additional paratypes indicated in the list of material examined.

Diagnosis.—A large species of the Mesochorea group characterized particularly by the very large prostate gland, which surpasses the spermiducal gland in both length and diameter. Spermiducal gland without a large subterminal posterior deferent lobe.

Description.—Body moderate to fairly large, ranging from 2.8-4.2 mm. in length, the greatest diameter occurring at segment vii, tapering gradually cephalad to segment i which is considerably narrower than the head; latter as long as the first three body segments combined; sucker appreciably broader than the two preceding segments, and as broad as the head.

Subsegments of the body of equal diameter, the prosomites about twice as long as metasomites. Most body segments of about the same length, except segment vii is longer than the others, and ix and x are slightly shorter.

Head rather long (about equal to first three body segments) and cylindrical, without subsegmentation except for the pronounced constriction at the base of the peristomium. Latter about a third the total head length and distinctly flared, its margin entire and unlobed. Jaws of moderate to fairly large size, subequal to each other in length and width, the dental formula 5–4.

Male reproductive system of moderate size, occupying about half of the area of one side of the sixth segment. Bursa small and subpyriform, as broad as long, or slightly broader; ejaculatory duct about

FIGURE 13.—Distribution of *Cambarincola mesochorea*. The records for Massachusetts unquestionably represent an adventitious occurrence, see discussion in text, p. 310.

equal to bursa in length, its diameter half or more the diameter of the spermiducal gland. Latter long and slender, entally somewhat enlarged and recurved ventrad over the bursa, the entry lobes of the deferent ducts terminal and equal in size. Prostate very large, at least as broad as spermiducal gland, usually of considerably greater diameter, and of equal length, its ental part normally curved mesiad under the gut and behind the spermiducal gland, and thus not visible. In normally distended specimens both the spermiducal gland and prostate lie oriented in a plane parallel to the median longitudinal axis of the body and extend the entire length of the coelom of segment VI.

Spermatheca rather slender, elongate, subfusiform, curving dorsolaterad around the gut, expanding laterally, and attenuated to a blunt ental process near the middorsal portion of the segment.

VARIATION.—Despite the rather extensive distribution of this species, I have been able to detect nothing of significance in the way of geographic variation in body form, jaws, or reproductive system. The single specimen seen from Louisiana differs somewhat from the

normal in having a distinctly broader ental portion of the prostate, as illustrated, but the quality level of this departure, particularly as seen in one specimen, cannot be given much attention at the present. It will, of course, be worthy of investigation when additional material is forthcoming from the lower Mississippi drainage.

Despite the apparent discontinuity involved, the specimens recorded from western Massachusetts do not vary in any way from the typical population of the species in Indiana.

DISTRIBUTION.—Records based upon specimens personally examined indicate a rather wide but perfectly coherent range over much of midland United States, from northern Michigan and South Dakota, Indiana, Kentucky, and Oklahoma to the coastal plain of Louisiana and Texas. No material has been examined from many of the States included in this general statement, but there is no doubt that future collections will establish the species in all of them, as well as extend the presently known periphery.

MATERIAL EXAMINED.—25 slides, from the following localities:

ARKANSAS: CRITTENDEN COUNTY: 14.6 miles south of Marked Tree, on U.S. Hy. 63, July 5, 1958, P. C. Holt (PCH 758). GREENE COUNTY: Roadside ditch along Ark. Hy. 25, 0.8 miles east of the Lawrence County line, July 5, 1958, Holt (PCH 759), MARION COUNTY: Fallen Ash Creek at Flippen, July 6, 1958, Holt (PCH 764).

INDIANA: CLAY COUNTY: 1.4 miles south of the Parke-Clay county line on Ind. Hy. 59, July 26, 1958, Holt (PCH 808). PERRY COUNTY: Small gravelly stream, 1.5 miles east of Adyville, U.S. Hy. 460, July 26, 1958, Holt (PCH 815, paratypes). SPENCER COUNTY: Sluggish muddy stream, 5.4 miles south of Chrisney on U.S. Hy. 231, July 27, 1958, Holt (PCH 817).

IOWA: DUBUQUE COUNTY: 9.9 miles north of St. Donatus on Iowa Hys. 28 and 67, May 12, 1956, Holt (PCH 896).

KANSAS: CHAUTAUQUA COUNTY: 4.3 miles west of the Montgomery County line, near Niotaze, July 8, 1958, Holt (PCH 773).

KENTUCKY: LOGAN COUNTY: Small stream at Diamond Spring, 5.7 miles north of Lewisburg on U.S. Hy. 430, July 27, 1958, Holt (PCH 821). MCLEAN COUNTY: 3.6 miles north of Livermore on U.S. Hy. 431, July 27, 1958, Holt (PCH 818).

LOUISIANA: ST. MARY'S PARISH: Lake Lapoudre at Morgan City, data and collector not indicated (USNM 17759). Identified as *C. macrodonta* by Max M. Ellis.

MASSACHUSETTS: BERKSHIRE COUNTY: Housatonic River drainage, Greenwater Pond, June 11, 1953, D. W. Crocker (PCH 577); also Lake Mahkeenac, same date and collector (PCH 578).

MICHIGAN: CHEBOYGAN COUNTY: Douglas Lake, July 1915, Max M. Ellis (USNM 17668). Labeled as paratype of *Cambarincola vitrea* by Ellis.

OKLAHOMA: COMANCHE COUNTY: Cache Creek at White Wolf Crossing, in Fort Sill, June 1, 1959, J. W. Berry (PCH 906). DELAWARE COUNTY: Small gravelly stream, 5.5 miles north of Jay, July 7, 1958, Holt (PCH 770).

SOUTH DAKOTA: BEADLE COUNTY: 6.6 miles west of the junction of Hys. 14 and 281, on U.S. Hy. 14, July 19, 1958, Holt (PCH 788). CODINGTON COUNTY: Watertown, July 19, 1958, Holt (PCH 789).

WISCONSIN: DANE COUNTY: Lake Mendota in Madison, August 28, 1949, A. A. Leath (PCII 262). JUNEAU COUNTY: 17 miles southeast of Mouston on U.S. Hy. 16, July 22, 1958, Holt (PCH 796).

Although these records give us but a general idea of the distribution, several inferences on peripheral limits can be drawn.

The distribution of the species in Kentucky appears to be essentially as now known. The rather intensive traverse of the State made by Dr. Holt in 1958 disclosed its presence in only two localities in the lower part of the Green River drainage. Further east, in Barren, Hart, and Edmondson counties, the species was apparently replaced by an abundant member of the Philadelphica group. The apparent absence of *mesochorea* from northern Indiana is more puzzling, there being no reason why the species should not occur in the headwaters of the Illinois River system. Yet the north-south traverse of western Indiana made by Dr. Holt in July 1958, failed to reveal specimens north of the latitude of Terre Haute. Clearly much more field work needs to be done in the States of Illinois, Indiana, and Michigan.

The records for western Massachusetts are almost certainly the result of the introduction by man of the common midwestern crayfish *Orconectes immunis*. Numerous collections from all parts of New York State made by Denton W. Crocker contain no specimens of *mesochorea*.

Presumably this species has a very wide range of ecological tolerance. It has been collected from numerous species of crayfishes in the genera *Procambarus* and *Orconectes*, in habitats ranging from natural and artificial lakes through roadside swamps and ditches to moderately cool gravelly streams. Whether *C. mesochorea* prefers a particular microniche on its hosts is at present unknown, but the question could easily be settled by an investigator collecting almost anywhere in the upper Mississippi Valley, where this species appears to be perhaps the most abundant member of its genus.

REMARKS.—The general body outline, head shape, and other characteristics give this species a strong superficial resemblance to *Cambarincola macrodonta* Ellis. It is not surprising that, relying upon jaw and body form for identification, Ellis should have misidentified a Louisiana specimen as *macrodonta*, but it is remarkable that he could have included such a conspicuously large-jawed creature as *mesochorea* among the paratype series of his own *vitrea*, which was diagnosed in part by its small and homodont jaws. Doubtless a number of existing literature records for *macrodonta* and *philadelphica* are actually based upon the present species. I have, however, made no attempt to piece together any information of this sort from published works.

The existence of Pierantoni's old name *Branchiobdella americana* constitutes the major threat to the validity of *mesochorea*. So far as the description goes, it applies quite well to *mesochorea*, *macrodonta*, *philadelphica*, and perhaps *chirocephala*. Reference of *americana* to the European genus *Branchiobdella* is surely based upon nothing more than Pierantoni's assumption of generic identity—*americana* being proposed prior to Ellis's establishment of the genus *Cambarincola*. As no material (aside from a single collection from New York reported by Goodnight) of a branchiobdellid with only one pair of testes has ever been seen from North America, and since recent morphological studies indicate that *Branchiobdella* is doubtless a Palearctic genus, I do not think that *B. americana* will prove to be other than some widespread and well-known species of *Cambarincola*. Pierantoni's types came from Texas and North Carolina and probably represent at least two species. Restudy of his slides and selection of a lectotype for the species may indeed show the priority of the name *americana* over *mesochorea*, but until this can be accomplished it is desirable to have a name available for the designation of this distinctive species.

MACROCEPHALA GROUP

The two species presently comprehended by this heading present such an array of basic similarities that their close relationship seems indisputable. One of the species is endemic to the Snake River drainage of Wyoming and Idaho, while the other is apparently localized in central Kentucky. Although the final word concerning the knowledge of this relationship remains to be written, some preliminary remarks may be of interest.

The group is characterized by (1) large size of body, and especially of the head, (2) a distinctive form of peristomial tentaculation, (3) short body segments of considerable diameter, having the effect, in the genital segments, of compressing the sex organs into a vertical alinement, (4) a large, globose bursa and relatively long ejaculatory duct, and (5) a very long spermiducal gland, entally bilobed at the entry of the deferent ducts.

Such characters are best appreciated by reference to illustrations, but attention is called in particular to the form of the peristomium. In most "tentaculated" species of the genus, the dorsal half of the peristomium is produced into four marginal lobes of greater or lesser dimension, the culmination being reached in *C. fallax* in which the lobes are fairly long and slender. In the present group, however, the tentacles are much more slender, and are submarginal in origin, resulting in a completely different appearance (see figures 15 and 18).

Key to Species of the Macrocephala Group

1. Ejaculatory duct very long, extending from bursa to nearly the middorsal region, spermiducal gland and prostate straight, extending dorsoventrally; head very large, up to a third the total length of the animal (Wyoming and Idaho) . . . . . **Cambarincola macrocephala** Goodnight

   Ejaculatory duct shorter, extending only halfway up the segment, the spermiducal gland and prostate thereby strongly bent, in their ectal third, downward to connect with it; head smaller, much less than a third of the total length (Kentucky) . . . . . **Cambarincola holti,** new species

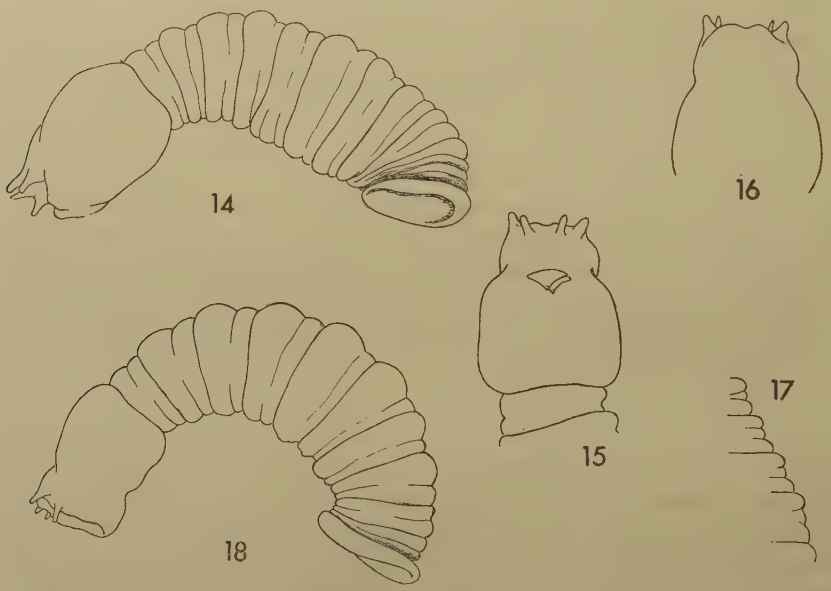
Cambarincola macrocephala Goodnight

FIGURES 14–17, 19

Cambarincola macrocephela [sic] Goodnight, 1943, Journ. Parasitology, vol. 48, p. 188.

Cambarincola macrocephala Holt and Hoffman, 1959, Journ. Tennessee Acad. Sci., vol. 34, p. 103.

TYPE SPECIMEN.—Holotype, USNM 20598, from *Pacifastacus g. gambelii* collected in Polecat Creek, northern Teton County, Wyoming, by Robert C. Brown, August 16, 1941. This large worm is mounted flattened dorsoventrally, and it is not possible to make out the reproductive systems with assurance.



FIGURES 14–18.—External appearance of two species of the Mesochorea section. 14, *Cambarincola macrocephala* Goodnight, lateral aspect, specimen from Gooding Co., Idaho. 15–17, *C. macrocephala,* type specimen, Teton Co., Wyoming: 15, Head in dorsal aspect with outline of jaws shown; 16, head in ventral aspect; 17, lateral profile of segments III–VI. 18, *C. holti,* lateral aspect, holotype, Pulaski Co., Kentucky.

DIAGNOSIS.—A large species of the Macrocephala group with a broad, enlarged head, tentaculate peristomium, isomorphic and similar jaws, large globose bursa, very long ejaculatory duct, long reflexed spermiducal gland with large symmetrically disposed ental deferent lobes, and an equally large reflexed prostate gland, extending ventrad to the level of the deferent lobes.

DESCRIPTION.—Maximum size of preserved worms, 4.8 mm. in length, 0.8 mm. in diameter at segment VII, and 1.1 mm. in greatest head width. Body outline of the usual profile, increasing in diameter up to segment VI, thereafter decreasing more abruptly to the penultimate segment.

Body segments very short in proportion to their diameter, the ratio about 4/1 to 5/1; prosomites about twice as long as metasomites and of slightly greater diameter.

Head very large, as long as the first five body segments combined (the entire anterior half of the body), its diameter as great as that of the broadest body segment. Peristomium not set off by a basal constriction nor strongly flared (at least in the material at hand), but divided into dorsal and ventral halves, the dorsal provided with four distinct slender submarginal tentacles, the ventral broadly bilobed.

Jaws large and robust, very similar in both size and shape, the dental formula 3–3; both jaws much wider than their length.

Male reproductive system large, occupying one entire side of the coelom of segment VI and extending mesad to the midventral and middorsal areas. Bursa very large and globose, as broad as long, the penial sheath occupying the ental half and normal in structure for the genus. Ejaculatory duct very long, extending dorsolaterad around the gut and somewhat dorsomesad to the junction of spermiducal and prostate glands. Both of the latter are then reflexed ventrad, curving around the gut down to the level of the penial sheath, where the spermiducal gland is evenly divided into two very similar deferent lobes which proceed ventromesad around the bursa to merge with the deferent ducts. Prostate similar in length and diameter to spermiducal gland, entally it is broadly rounded and completely overlaps the caudal deferent lobe.

VARIATION.—The available material from Idaho is quite homogeneous and presents only the size variation that one would expect in a single collection.

The holotype of *macrocephala*, mounted flat on a slide, differs somewhat from the specimens described in that the peristomium is set off by a basal constriction, with the tentacles somewhat smaller both in length and diameter. These differences may be due to preservation in strong alcohol. On the other hand, some of the anterior segments of the type specimen, notably from III through VI, are quite

distinctly tripartite, and suggest the condition upon which Goodnight founded a genus *Triannulata*. More caudal segments appear normal, e.g., with two subsegments.

Relationships.—The affinities of *macrocephala* lie rather clearly with the very similar *C. holti* from central Kentucky, which differs in its smaller size, particularly that of the head, and longer glandular organs of the male reproductive system. That the similarities of the two are due to convergence seems unlikely, and it is possible that we are here confronted with two relict forms of a parental stock which extended widely across North America during mid-Tertiary times.

Distribution.—Known only from two widely separated localities in the upper part of the Snake River drainage. Collected, in addition to the type locality, at the following station:

Idaho: Gooding County: Riley Creek at the Idaho Fish Hatchery, July 14, 1958, P. C. Holt (PCH 785). At this locality it occurred on *Pacifastacus gambelii connectans*.

Remarks.—Assignation of the Idaho specimens to Goodnight's name *macrocephala* is made here with some reservation. Several differences shown by the type of the species have been noted in a preceding paragraph, and are illustrated in the accompanying figures. Until fresh topotypes of *macrocephala* are obtained for study, there will remain some doubt about its identity, but the general similarity of the worms from the two localities is so great that I think a conservative approach is warranted here. Although the male sex organs of the holotype can be seen only in dorsal aspect, they seem to correspond to those of the specimens from farther down the Snake River.

Presumably the original spelling "*macrocephela*" is due to a typographical error. The meaning, "long-headed" is particularly appropriate for a worm in which the head is one-third the entire length of the animal!

Cambarincola holti, new species

Figures 18, 20

Type specimens.—Adult holotype and paratypes of various ages, USNM 29940, from *Cambarus* sp. collected in a stream on the southern edge of Somerset, Pulaski County, Kentucky, by Perry C. Holt, July 28, 1958.

Diagnosis.—A moderately large worm generally similar to *macrocephala* in body form and proportions, but distinct in the dental formula (5–4), abruptly flexed spermiducal and prostate glands, and characteristically shaped spermatheca.

Description.—Maximum size of preserved worms (holotype), 4.1 mm. in length, 0.9 mm. in diameter at segment VIII, 0.7 mm. in greatest head width. Body outline of the usual form, segments V-VII of es-

FIGURES 19, 20.—Reproductive systems, lateral aspect, of two species of the Mesochorea section. 19, *Cambarincola macrocephala* Goodnight, specimen from Gooding Co., Idaho. 20, *C. holti*, new species, paratype, Pulaski Co., Kentucky. Drawings to same scale.

sentially equal diameter; segment I the smallest. Body segments short, as little as a fourth the diameter at midbody, as much as a half at anterior end; prosomites large, about three times as long as metasomites. Caudal sucker large, its diameter greater than that of head.

Head larger than normal for genus, as long as first three body segments combined, and about a fourth the entire length of the animal, broader than the first segment but considerably narrower than midbody segments. Peristomium distinctly set off by a basal constriction, about a third of the total head length, with four slender elongate dorsal tentacles slightly removed from the peristomial margin, each subtended by a small rounded lobe.

Jaws large and massive, equal in size but anisomorphic, the dental formula 5–4 or 3–4.

Male reproductive system large, occupying most of one side of the coelom of segment VI as well as the midventral and middorsal areas. Bursa large and subglobose, a little longer than broad, merging entally into a short, slender, ejaculatory duct. Latter entering spermiducal gland at about the middle of the segment, the gland continuing dorsad for about a third of its length and then strongly bent on itself and directed ventrad to the level of penial sheath where

it bifurcates into the large deferent lobes which then proceed ventromesad into the deferent ducts. Prostate gland similar in length, diameter, and external appearance to the spermiducal gland, and likewise is directed entally first dorsad and then ventrad, crossing over the flexed part of the spermiducal gland in changing its direction; extending ventrad to level of the posterior deferent lobe.

Spermatheca is composed of three distinct sections: The basal or ectal half is an elongate, sinuous, muscular duct merging into a somewhat enlarged, subglobose, clear-walled ental bulb, this in turn gives origin to a smaller, tubular, and strongly glandular ental process, terminating in a rounded, somewhat swollen tip.

VARIATION.—This species is known only from a single collection of about a dozen worms, these vary among themselves only in size and proportions. In smaller worms, the dental formula is more consistently 5–4, the outermost lateral cusps of the dorsal jaw tending to be worn away in old specimens.

AFFINITIES.—Among known species of the genus, this one is obviously closest to *C. macrocephala*, and the differences between the two are largely set forth in the diagnoses and in the key. The presence of distinct tentacles will easily preclude confusion of *holti* with *mesochorea*, the only other eastern member of the section of comparable size and with very large, undifferentiated prostate gland.

DISTRIBUTION.—Known only from the type locality, "a medium large mountain stream" on the southern outskirts of Somerset, Kentucky. Perhaps it thus partakes of the characters of a more mountainous habitat than might be expected in south central Kentucky. It is unusual that numerous other collections made in the same general region on the same day did not yield specimens of this form. That it is endemic to a single stream seems unlikely, and the resolution of its distribution and ecology stands as a challenge to some future student of the genus.

REMARKS.—*C. holti* was taken in association with species in the genera *Pterodrilus* and *Xironodrilus*. The type specimen and some of the paratypes are rather heavily infested with stalked colonial peritrich protozoans, much more than any other specimens examined during this study.

BRANCHIOPHILA GROUP

This group embraces two species of somewhat dissimilar worms, and may have to be abandoned when the genus becomes better known. Both of the species are small and although generally similar in structure may not share a common origin.

In this group the spermiducal gland is of normal relative size and proportions, and produced into a large terminal or lateral posterior

deferent lobe. The prostate is rather short and histologically similar to the spermiducal gland. There are no appreciable specializations aside from the modification of the nominotypical species for inhabiting the branchial chambers and gills of the crayfish.

It is here that we encounter extremely localized forms: Each of the species is known only from one locality. Their specific distinctness certainly suggests that they must be relicts of a former wide-ranging stock, rather than recent derivatives of an existing progenitor.

Cambarincola branchiophila Holt

FIGURES 23, 24

Cambarincola branchiophila Holt, 1954, Virginia Journ. Sci., new ser., vol. 5, pp. 168–172, figs. 1–5.—Holt and Hoffman, 1959, Journ. Tennessee Acad. Sci., vol. 34, p. 103.

TYPE SPECIMENS.—Holotype, USNM 25855, from *Cambarus bartonii* and *C. sciotensis* collected in Sinking Creek, Giles County, Virginia (one mile west of Newport), by P. C. Holt, F. D. Kiser, and Cornelia Tuten, July 3, 1950; topoparatypes, PCH 407, from the same collection.

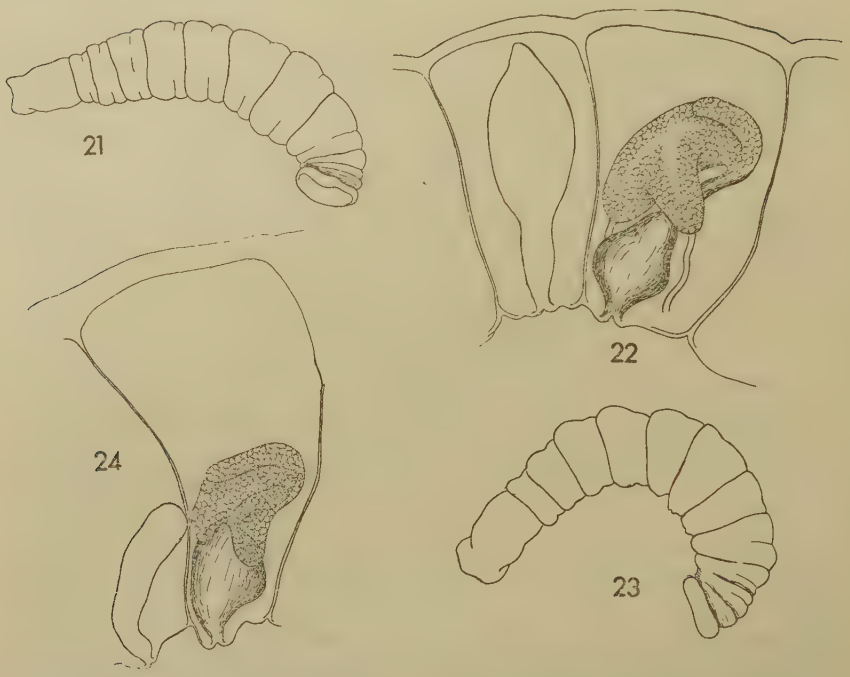
DIAGNOSIS.—A moderately large species of its group, characterized by the stout body form, 5–5 dental formula, and generally reduced male reproductive system, without the strongly shortened prostate gland which characterizes *Cambarincola shoshone*.

DESCRIPTION.—Body stout, up to about 3.5 mm. in length, segment I narrowest, following segments increasing up to VI and VII which are twice the diameter of I; last three body segments abruptly decreasing in size, caudal sucker subequal in diameter to segment I. Segments short, the prosomites about twice the length of metasomites but not elevated above them.

Head relatively small, only slightly longer than broad; its diameter less than that of segment I; peristomium set off by a distinct basal constriction, flared but with entire margins, no evidence of lobes in preserved specimens. Basal portion of head subdivided by a slightly impressed constriction and thereby appearing superficially tripartite in profile.

Jaws small, essentially isomorphic; heterodont, the dental formula 5–5 with the paramedian cusps of each jaw slightly smaller than the large median and outer dentations.

Male reproductive system reduced in overall size and confined to the lower third of one side of the segment. Bursa obovate to fusiform, about as long as the slender ejaculatory duct; spermiducal gland small, somewhat flattened, with two subequal deferent lobes; prostate gland fairly broad, slightly enlarged entally, extending as far as the sinus between the deferent lobes.



FIGURES 21–24.—Structural details of two species of the Mesochorea section. 21, *Cambarincola shoshone*, new species, paratype, Gooding Co., Idaho; 22, the same, reproductive systems in lateral aspect. 23, *C. branchiophila* Holt, paratype, Giles Co., Virginia; 24, the same, reproductive systems in lateral aspect. Figures 21, 23 and 22, 24 drawn to same scales.

Spermatheca simple, a slender tubular structure, with a fairly short, muscular ectal third and a slightly thicker glandular ental two-thirds; no ental process present.

VARIATION.—The only appreciable variation observed in the small number of worms available from the type locality affects the proportions of the bursa, specifically its length to diameter ratio. Presumably such variation is a consequence of muscular reaction to preservation.

AFFINITIES.—Superficially this species bears a strong resemblance to *C. shoshone*, although the similarity may be a result of convergence. In my opinion, *C. branchiophila* is a relict of some extinct ancestral stock, and does not have any really close relatives among the known existing species.

DISTRIBUTION.—Known only from the type locality, but certainly to be expected elsewhere in the Kanawha River drainage of southwestern Virginia.

REMARKS.—In the original description, Holt cites some measurements of interest. He found that the deferent ducts of this species

approximate 23 microns in diameter, while those of the somewhat larger *C. philadelphica* attained a diameter of only 14 microns in a considerable series of specimens measured. Probably the conversion of this data into some common ratio—such as duct diameter in relation to jaw length—would produce an even more dramatic separation.

This is the only member of the genus known to be branchiophilus, although *C. demissa* presumably is also. In general, our knowledge of such species is very deficient, owing to the usual necessity of dissecting the crayfish to extract and examine the gill tissue, and it is entirely reasonable to assume that greater attention to this neglected phase of collection will result in the discovery of additional gill-inhabiting forms.

Cambarincola shoshone, new species

FIGURES 2, 21, 22

TYPE SPECIMENS.—Holotype and three paratypes, USNM 29941, from *Pacifastacus gambelii connectans* collected in Riley Creek in the Idaho Fish Hatchery near Hagerman, Gooding County, Idaho, by Perry C. Holt, July 14, 1958. Topoparatypes from the same collection, PCH 785.

DIAGNOSIS.—A small species tentatively referred to the Branchiophila group, characterized by the distinct and equal-sized deferent lobes, the very short prostate, the very small, isomorphic, homodont jaws, and the graceful, even, body profile.

DESCRIPTION.—Maximum length, 1.8 mm., body smallest at segment I, gradually increasing in diameter to segment VII which is also the longest; caudal sucker moderate to large, wider than head or segment I, equal in diameter to segment II. Prosomites only about twice as long as metasomites, and of the same diameter, the intersegmental groove very weakly defined.

Head small, slender, about as long as first three body segments combined, narrower than segment III, distinctly divided into three subsegments by constrictions; peristomium set off by a very pronounced basal constriction, somewhat flared, divided into a small dorsal and a much larger ventral half but otherwise entire and not provided with dorsal lobes.

Jaws very small, less than 6 percent of the head length, isomorphic and homodont, the dental formula 3–3, each tooth large and conspicuous.

Male reproductive system of moderate size, extending dorsad as far as level of gut. Bursa of average relative size, strongly expanded from a narrow ectal portion, the circular muscle region enlarged; penial sheath likewise somewhat expanded as seen in profile. Ejaculatory duct fairly long and slender, shorter than length of bursa.

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Spermiducal gland larger than bursa, entally divided into two large, subequal deferent lobes, the posterior lobe directed caudoventrad and concealing ectal half of the ejaculatory duct and apex of penial sheath. Prostate quite slender and short, its histology similar to that of spermiducal gland, no terminal bulb detected.

Spermatheca tripartite, consisting of a slender muscular ectal duct, a somewhat translucent, globosely enlarged median sperm reservoir, and an abruptly set-off glandular ental process.

Variation.—All of the specimens examined are essentially similar in structural features, varying chiefly in size. The bulbar portion of the spermatheca varies considerably in its relative size and globosity, from merely fusiform to nearly sphaeroid appearance.

Affinities.—Of the known species of the genus, *shoshone* appears to be structurally most like *branchiophila*. That the relationship is due to convergence cannot, however, be discounted. Here the matter must rest until additional species have come to light.

Distribution.—Known only from the type locality, a tributary of the Snake River in the southwestern part of Idaho.

PHILADELPHICA SECTION

The species comprehended in this major subdivision of the genus include the most widespread and frequently encountered forms. Most of them are already known from a considerable number of localities, although a few appear to be localized. Resolution of specific identities in this section has proved to be the major problem in the revision, as the species in the Philadelphica group are generally similar and difficult to separate.

This section is characterized by the form of the male reproductive system. The prostate is histologically quite different from the spermiducal gland, being composed of large cuboidal cells containing little or no granular material and apparently with no well-defined nuclei. Entally, the prostate terminates in a clear bulbous development, the function of which is still unknown. Possibly it is related to some hydrostatic function of the prostate, as the relative size varies slightly in different individuals.

Within the limits set by the preceding definition, there is considerable variation in body form, size, jaw structure, and details of the sex organs. The range of variability in each category is as great as observed for the entire genus, reflecting perhaps considerable evolutionary radiation subsequent to the differentiation and specialization of the prostate, but in general the overall facies of all the species is basically similar and leaves little doubt about the homogeneity of the section.

As now understood, the twelve species may be conveniently allocated into five groups on the basis of characters taken in combination and indicative of close affinities.

Key to Groups of the Philadelphica Section

1. Prostate gland very long, much exceeding length of the spermiducal gland. (fig. 34), its terminal third slightly twisted or sinuate; very large species. INGENS GROUP (p. 333)
   Prostate gland never longer than the spermiducal gland and often much shorter; small to moderate-sized species 2
2. Spermiducal gland with a very large lateral (posterior) deferent lobe (fig. 36); prostate terminating in a somewhat rudimentary bulb. VIRGINICA GROUP (p. 321)
   Spermiducal gland without a conspicuous posterior deferent lobe; prostate terminating in a conspicuous bulb 3
3. Spermiducal gland very long, its ental half reflexed closely upon the ectal half; in lateral aspect this gland together with the prostate assuming a distinctly sigmoid alshape . . . . . VITREA GROUP (p.323)
   Spermiducal gland shorter, often strongly curved but never with the ental half turned back against the ectal half 4
4. Jaws strikingly dissimilar, the dorsal about eight times the bulk of the ventral; prostate gland about half as long as spermiducal gland or less; general size of the male reproductive system reduced; body size small to moderate. HETEROGNATHA GROUP (p. 361)
   Jaws either identical in size and shape, or anisomorphic with the dorsal jaw slightly the larger; prostate at least half as long as the spermiducal gland; reproductive system normal in size for the genus; body size moderate to large . . . . . PHILADELPHICA GROUP (p. 336)

VIRGINICA GROUP

This group is proposed to accommodate an interesting small worm, herein described as new, which casts some light on the possible antecedents of other members of the section. *Cambarincola virginica*, at first sight, appears to be related to *ouachita* and to *branchiophila* because of the large posterior deferent lobe of the spermiducal gland, yet magnification reveals that the prostate is distinctly differentiated and that the terminal bulb is present, in a rudimentary form. The jaws of this species are quite similar to those of species in the Vitrea group.

I suggest that in this worm we have an approximation to the ancestral form of the Philadelphica section shortly after the basic dichotomy which has given rise to the three major sections of the genus. The posterior deferent lobe is doubtless a primitive character which has become increasingly suppressed through the Philadelphica section concomitant with the emphasized differentiation of the prostate, and, also, the gradual reduction in bulk of the sex organs.

It is likewise a matter of interest that the species occurs in an area both geographically and ecologically remote from the main center of speciation in eastern United States.

Cambarincola virginica, new species

FIGURES 35, 36

TYPE SPECIMENS.—Holotype and paratype, USNM 29942, from *Cambarus acuminatus* collected in a small slow stream 4.7 miles north of Petersburg, Chesterfield County, Virginia, by P. C. Holt and M. L. Bobb, May 31, 1949.

DIAGNOSIS.—With the characters of the group, easily recognized within the genus by the combination of a specialized prostate with small terminal bulb and a large lateral deferent lobe near the middle of the spermiducal gland. The spermatheca is very long and slender, extending to the middorsal region.

DESCRIPTION.—A moderately small worm, up to 2.0 mm. in maximum length, the body profile very slightly fusiform with the greatest diameter at segment VII, gradually tapering toward each end; prosomites only slightly longer than metasomites and of about the same diameter. Caudal sucker wider than segment I and head.

Head rather small and short, only slightly longer than broad, of the same diameter as segment I, peristomium set off by a basal groove and somewhat flared, but essentially with entire margins. Jaws small, anisomorphic but equal in size, dental formula 5–4, teeth virtually subequal in size and shape, the median dorsal or paramedian ventral teeth slightly the largest.

Male reproductive system large, filling one side of the segment lateral to the gut. Bursa elongate fusiform, 1.5 to 2 times as long as broad, about equally divided into atrium and penial sheath, merging abruptly into the slender ejaculatory duct. The latter a little more than half as long as bursa, and slightly enlarged at its midlength. Spermiducal gland large, directed obliquely cephaloventrad across the segment, extending down to the level of midlength of the bursa, thence merging into the anterior deferent lobe which proceeds mesad into the segment. Posterior deferent lobe large and distinct, from the midlength of the gland, directed caudad and concealing most of the ejaculatory duct, beyond which it is bent abruptly ventromesad, merging into the posterior deferent duct. Prostate gland about two-thirds the maximum diameter of the spermiducal gland, but less than half its length, composed of large vacuolated cuboidal cells very different from the cells of the spermiducal gland; terminating in a small and inconspicuous clear space doubtless homologous with the large bulb of the Philadelphica group.

Spermatheca elongate, slender, extending up around the gut as far as the middorsum of the coelom, not appreciably enlarged along its length but divided into three general regions, viz, an ectal glandular spermathecal duct, a median (presumably distendable) bulbar portion, and an ental process composed of thick cuboidal epithelium.

Variation.—The small quantity of specimens examined is essentially homogeneous in all diagnostic characters.

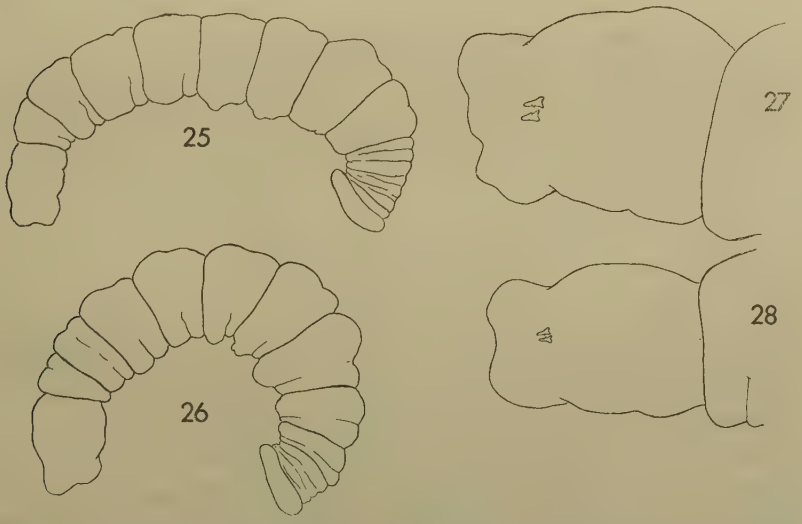
Affinities.—Not closely related to other members of the section. The gross appearance of the genital organs is somewhat like that of some species of the Mesochorea section, notably *Cambarincola ouachita*, but the histology of the prostate is an easily seen fundamental distinction.

Distribution.—Known only from several streams in the Fall Line belt in eastern Virginia, to which region it may perhaps be endemic. Aside from the type locality, specimens of this species are at hand from one additional station:

Virginia: Chesterfield County: Stream below the lake in Camp Shawandasee, May 14, 1949, P. C. Holt (PCH 211), from *Cambarus acuminatus* Faxon.

VITREA GROUP

The two species referred to this group are quite similar in most respects and may eventually be shown to be geographic races of a single, wide-ranging form.



Figures 25–28.—Structural details of two species of the Vitrea group. 25, *Cambarincola vitrea* Ellis, specimen from Sumner Co., Kansas. 26, *C. osceola*, new species, specimen from Calhoun Co., South Carolina. 27, *C. osceola*, head in lateral aspect, jaws shown in outline, 7.8 percent of head length. 28, *C. vitrea*, head in lateral aspect, specimen from Beadle Co., South Dakota, jaws shown in outline, 4.8 percent of head length.

The outstanding characteristics of the Vitrea group lie in (1) the anisomorphic, essentially homodontous small jaws, and (2) the strongly sigmoid shape assumed by the thick prostate and the long, reflexed spermiducal gland.

Whether actually two different species, or only subspecies, the two forms of this group are interesting in exhibiting a certain amount of geographic variation in the jaw size and proportions. As discussed at length under the treatment of *C. osceola*, the size of the jaws relative to head length varies in a general gradient from northwest to south and thence northeast again. Furthermore, over most of the combined range, the ventral jaw is subequal to the dorsal or slightly longer, while in the northern segment of *osceola* the dorsal jaw becomes distinctly longer than the ventral.

The ranges of both forms coincide generally with lowland habitats, a circumstance which in many cases appears to enhance wide distribution by affording a sort of ecological continuity.

The following key will separate 100 percent of the specimens which have been examined. The future student of this group is cautioned that well-preserved specimens are essential for making accurate measurements, and that material from the Gulf Coast States may be expected to show some degree of intermediacy.

Key to Species of the Vitrea Group

1. Prostate gland larger in diameter, from 70–90 percent of the diameter of the spermiducal gland at the base, averaging 82 percent; length of longest jaw 5–7 percent the length of the head (interior United States in the Mississippi River drainage . . . . . **Cambarincola vitrea** Ellis

   Prostate gland smaller in diameter, from 50–70 percent of the diameter of the spermiducal gland at the base, averaging 56 percent; length of longest jaw 7–9 percent of the head length (Atlantic and Gulf Coastal Plain region). **Cambarincola osceola,** new species

Cambarincola vitrea Ellis

FIGURES 25, 28, 29, 31

Cambarincola vitrea Ellis, 1918, Pap. Michigan Acad. Arts Sci., vol. 37, p. 51; 1919, Proc. U.S. Nat. Mus., vol. 55, p. 249.—Goodnight, 1940, Illinois Biol. Monogr., vol. 17, No. 3, p. 33; 1943, Journ. Parasitology, vol. 48, p. 188.—Holt and Hoffman, 1959, Journ. Tennessee Acad. Sci., vol. 34, p. 103.

TYPE SPECIMEN.—Holotype, USNM 17667, from *Orconectes immunis* collected at Douglas Lake, Cheboygan County, Michigan, by Max M. Ellis in July 1915. This specimen is mounted flattened dorsoventrally, showing the jaws clearly; the reproductive systems are obscured, however.

DIAGNOSIS.—A moderate-sized member of the genus, easily recognized by the characters of the body form, jaws, and especially the

FIGURES 29, 30.—Reproductive systems of two species of the Vitrea group. 29, *Cambarincola vitrea* Ellis, specimen from Dane Co., Wisconsin. 30, *C. osceola*, new species, specimen from Southampton Co., Virginia.

strongly sigmoid spermiducal gland of the male reproductive system and the elongate spermathecal duct with a small globose ental bulb.

DESCRIPTION.—Moderate in body size, ranging from 1.9 to 2.6 mm. in length, the greatest diameter occurring at segment VII which is only slightly broader than segments V and VI; prosomites only of very little or not of greater diameter than the metasomites.

Head somewhat smaller than average for the genus, equaling segment I or less in diameter, its length somewhat less than diameter of segment VII. Peristomium distinctly set off by a constriction, flared, both upper and lower major lobes simple; ventral side of head usually with an additional transverse constriction near the base.

Jaws small, heterodont, dissimilar in dorsal aspect with a 5–4 dental formula but very similar in lateral aspect and approximately of the same size. Dorsal jaw with five widely separated acute cusps of which the median and two paramedian members are of about the same size, the two lateral cusps slightly smaller. Ventral jaw with

four similar dentations, the paramedians a little larger than the laterals. In lateral aspect the dorsal jaw averages 6.1 percent of the total head length, with variation from 4.8–7.2 percent.

Body of normal proportions for the genus, segment I somewhat broader than head diameter, the body increasing gradually back to segment VI and VII, thence tapering rather abruptly to X which is distinctly narrower than the caudal sucker. Latter fairly large, either equally (rarely) or slightly exceeding (usually) the greatest head diameter.

Male reproductive system (fig. 29) fairly large in its relative size, occupying most of one side of segment VI. Bursa pyriform or subcordate in shape, 1.5 times as long as broad or even less. Atrial portion shorter than penial sheath. Ejaculatory duct short and narrow, one-half to two-thirds as long as bursa and about a fourth as wide. Spermiducal gland very long and abruptly reflexed at the midlength, the ental half lying beside and against the ectal with the ental end overlapping the bursa. No enlargement or lobation of the gland at points of entry of the very slender deferent ducts. Prostate relatively short and slender, less than two-thirds as long as spermiducal gland, and about three-fourths its diameter, with a well-defined terminal bulb.

Spermatheca elongate and slender, curving dorsolaterad around the gut in segment V and attaining the middorsal interior wall of the segment. Basal two-thirds composed of the parallel-sided and slender spermathecal duct, the ental third of the globose or fusiform spermathecal bulb. No ental glandular process present.

VARIATION.—A certain amount of variation affecting the relative size and proportions of the sexual organs was detected, but none of it appears to be associated with any sort of morphocline. A possible geographic gradient may affect the jaw size—specimens from Kansas have appreciably larger jaws which measure from 6–8 percent of the head length, whereas worms from Wisconsin and South Dakota (somewhat larger in total size) have jaws with a length only 5 percent that of the head. Presumably material from the intervening region will be found to be intermediate in this respect. The shape of the jaws is not affected by this variation in size. A summary of selected measurements is appended in a following table which compares this form with *C. osceola*.

AFFINITIES.—The only close relative of *vitrea* is the form hereinafter described under the name *osceola*. So far as existing material goes, *osceola* differs clearly from *vitrea* in jaw size and details of the sex organs, but the accumulation of specimens from the Gulf Coast region may reveal the presence of intermediate populations.

FIGURE 31.—Distribution of the two species of the Vitrea group. ○, *Cambarincola vitrea;* ●, *C. osceola.* Symbols represent the localities from which specimens have been examined; no literature records included.

DISTRIBUTION.—On the basis solely of material personally examined, *vitrea* is found to be widely distributed in the upper Mississippi Valley and Great Lakes region, and various published records (some doubtless incorrect) extend the range even more broadly. As presently known, the range of *vitrea* extends from the Red River in Arkansas north to the Great Lakes, and from Michigan and Illinois west to the foothills of the Rockies.

Presumably the species may be found in Indiana, but it was not represented in any of the collections made by Dr. Holt in a north-south traverse of that State in 1958. It may be found that the population of northern Michigan arrived by crayfish from the west across the Straits of Mackinac during the postglacial occupation of Wisconsin.

Future collectors will have plenty to do in rounding out our knowledge of the distribution of this easily recognized species. Existing confirmed records are those of the following collections:

COLORADO: BOULDER COUNTY: St. Vrain's Creek near Boulder, May 1915, Max M. Ellis (USNM 17670, 4 slides). YUMA COUNTY: Arikaree River near Beecher's Island, October 1915, B. Jaffa (USNM 17677, 2 slides).

OKLAHOMA: COMANCHE COUNTY: Fort Sill, June 6, 1959, J. W. Berry (PCH 905).

ARKANSAS: BENTON COUNTY: Wildcat Creek at Ark. Hy. 68, July 7, 1958, P. C. Holt (PCH 769). CRITTENDEN COUNTY: 14.6 miles south of Marked Tree on U.S. Hy. 63, July 5, 1958, Holt (PCH 758). GREENE COUNTY: 0.8 miles east of the Lawrence County line on Ark. Hy. 25, July 5, 1958, Holt (PCH 759).

KANSAS: CHAUTAUQUA COUNTY: 4.3 miles west of the Montgomery County line on Kans. Hy. 166, July 8, 1958, Holt (PCH 773). LYON COUNTY: 3.5 miles west of Emporia, June 2, 1944, Zirnstein (PCH 182). SUMNER COUNTY: 5.6 miles north of South Haven on U.S. Hy. 81, July 8, 1958, Holt (PCH 775).

ILLINOIS: CHAMPAIGN COUNTY: Urbana, Frank Smith (USNM 17676). IROQUOIS COUNTY: Wellington, September 1914, A. T. Stevens (USNM 17675).

MICHIGAN: CHEBOYGAN COUNTY: Douglas Lake, summer 1915, Max M. Ellis (USNM 17668, paratypes, 17673, 17675).

MINNESOTA: OLMSTEAD COUNTY: 5.9 miles west of Eyota on U.S. Hy. 14, July 21, 1958, Holt (PCH 792). WRIGHT COUNTY: Clearwater River at Minn. Hy. 152 in town of Clearwater, July 21, 1958, Holt (PCH 793).

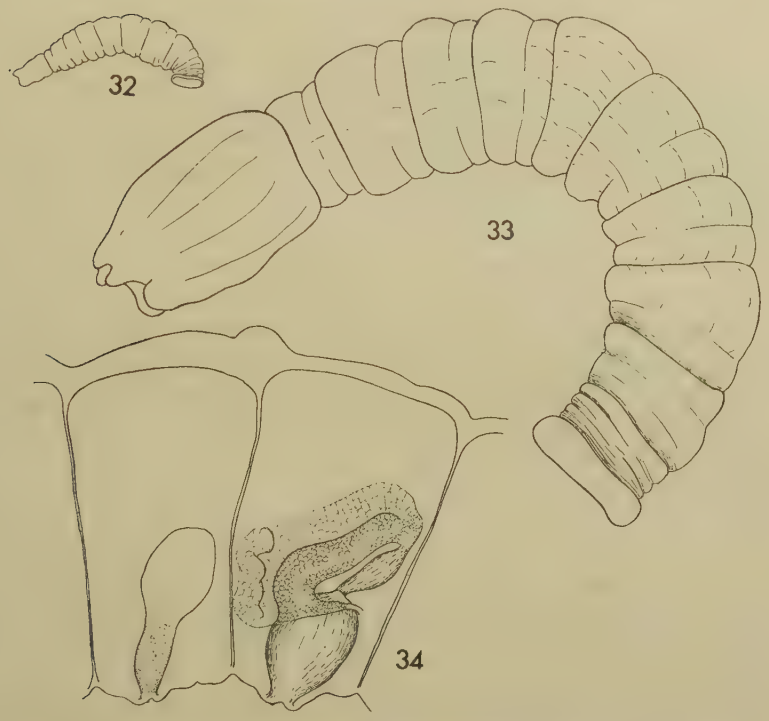
WISCONSIN: DANE COUNTY: Lake Mendota in Madison, August 28, 1949, A. A. Leath (PCH 262). GRANT COUNTY: Blake Fork, on Wis. Hy. 35 near Bloomington, May 13, 1956, Holt (PCH 900). JUNEAU COUNTY: 17 miles southeast of Mauston on U.S. Hy. 16, July 22, 1958, Holt (PCH 796). ONEIDA COUNTY: Rhinelander, October 1915, G. Hanson (USNM 17669, 5 slides).

SOUTH DAKOTA: BEADLE COUNTY: 3.4 miles east of Wessington on U.S. Hy. 14, July 19, 1958, Holt (PCH 788).

REMARKS: This widespread and often abundant species was originally described in the body of a key to four species of branchiobdellids collected by Ellis in Michigan, with the indication that the formal description was then in progress. The name *vitrea* is usually cited as dating from 1919, although the earlier usage constitutes a valid proposal of a new name, containing as it does considerable comparative description with related forms and general indication of a type locality.

In the following year the complete description of *vitrea* was published, including a photograph of the entire animal, drawings of the jaws, and an imposing list of localities from the Middle West and Great Plains areas. The species appears not to have been mentioned again in the literature until the publication of Goodnight's summary of 1940, which merely quotes the original description with its published localities, and adds 23 new localities for the species. The only new and original commentary contributed is the remark that "This form could be confused with *Cambarincola macrodonta* but it is easily distinguished by the difference in tooth structure as outlined above." Presumably the dimension of 310 mm. cited by Goodnight for the holotype is a misprint for Ellis's original figure of 3.0 mm.

In three other short papers, Goodnight has recorded *vitrea* from Georgia (1940b), Florida (1941), and Wyoming and Michigan (1943).



FIGURES 32–34.—Structural details of two species of *Cambarincola*. 32, *C. shoshone*, new species, body profile, drawn to same scale as next figure to show difference between the smallest and largest species in the genus. 33, *C. ingens*, new species, body in lateral aspect, paratype, Giles Co., Virginia; 34, reproductive systems of the same specimen.

Woodhead (1950) has published a figure of a branchiobdellid from Michigan identified by him as *vitrea*, but it is obvious that his species is not even congeneric with Ellis's.

Ellis emphasized a superficial resemblence in body form between *vitrea* and *Xironodrilus formosus*, in which I concur. He also pointed out, correctly, the distinctive characters of the small, acutely toothed jaws, but curiously enough one of his paratypes from Douglas Lake is a perfectly typical specimen of the new species *C. mesochorea*, having jaws entirely different in size and shape from the other specimens of the type series!

The name *vitrea* was given by Ellis with reference to the glassy appearance of the body wall of the type material. This may be a characteristic of the species in life, but in the preserved specimens which I have seen there is nothing unusual about the texture of the integument.

Cambarincola osceola, new species

FIGURES 26, 27, 30, 31

TYPE SPECIMENS.—Holotype and seven paratypes, USNM 29943, from *Procambarus paeninsulanus* and *Cambarus uhleri* collected along Dry Creek, 3.1 miles north of Iron City, Seminole County, Georgia, by Horton H. Hobbs and C. W. Hart, September 9, 1955.

DIAGNOSIS.—A small species of the Vitrea group, very similar to the typical species and possibly a geographic race of it, but differing in the much smaller diameter of the prostate in comparison with that of the spermiducal gland, as well as by differences in the jaw sizes at least in the populations of the two that are geographically most approximate.

DESCRIPTION.—Essentially similar in body form to *C. vitrea*, averaging perhaps somewhat larger (2.8 mm. in maximum length). Segments slightly more uniform in diameter, although the midbody segments (V–VII) are the largest; caudal sucker generally smaller than the head diameter.

Head larger than in *vitrea*, equaling or exceeding diameter of segment I, its length equal to diameter of segment VII. Peristomium distinctly set off and flared, its margin entire except for division into dorsal and ventral halves.

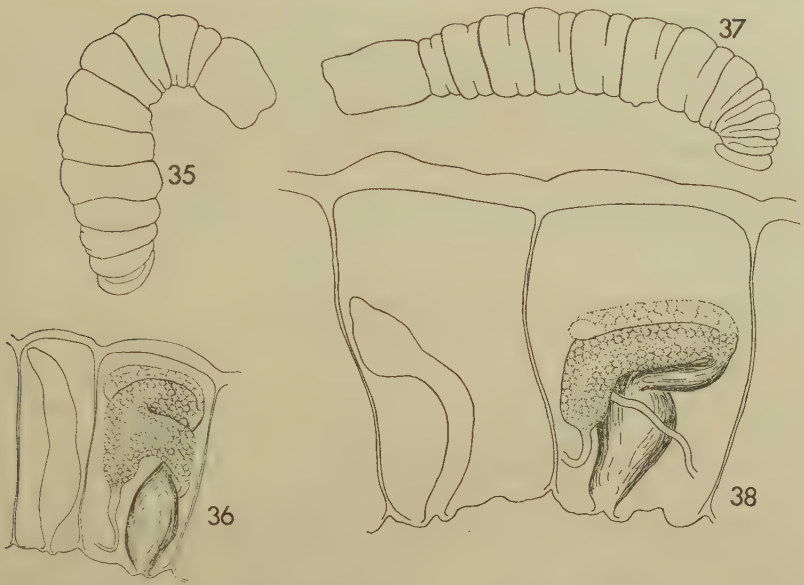
Jaws larger than in *vitrea* although of similar form, i.e., anisomorphic, pentatetradont, the individual teeth well separated and essentially homodont. In lateral aspect the jaws elongate and slender, the lateral cusps elevated and distinct. In specimens from Florida and Georgia, the jaws are subequal in length or the ventral jaw is longer; in more northern material (South Carolina to Virginia) the relationship is reversed with the dorsal jaw distinctly the longest.

Male reproductive system similar to that of *vitrea* in most respects, differing chiefly in the lesser diameter of the prostate gland in comparison with the spermiducal gland: from 50-70 percent the diameter of the latter as against 70-90 percent in *vitrea*.

Spermatheca with an elongate, slender, ectal duct which extends into the dorsal half of the coelom and a slightly enlarged ental bulb, the latter generally of greater size than in *vitrea*.

VARIATION.—Most of the observed variation within the limits of this form affect the actual and relative size of the jaws with respect to head length. Similar variation has been remarked in the treatment of *C. vitrea*.

In the population of southern Georgia and adjacent northwest Florida, the jaws are either of equal median length or the ventral jaw is slightly the longer, and averages from 6-8 percent of the total head length. In the segment of the species which occurs in Virginia



FIGURES 35–38.—Structural details of two species of *Cambarincola*. 35, *C. virginica*, external appearance of holotype, Chesterfield Co., Virginia (somewhat distorted in preservation); 36, the same, reproductive systems in lateral aspect. 37, *C. macrodonta* Ellis, lateral aspect of paratype, Boulder Co., Colorado; 38, the same, reproductive systems in lateral aspect.

and the Carolinas, the dorsal jaw is invariably the longer, amounting to 8 or 9 percent of the head length. There is unfortunately nothing available in the way of good material from north Georgia, so we cannot say whether this variation represents merely a north-south gradient or whether some break in the distribution of the character occurs (as possibly at the Savannah River). It will be recalled that in *vitrea*, variation in the ratio of jaw length to head length proceeds in just the opposite direction, the jaws becoming smaller in going north from Arkansas to North Dakota.

This relationship casts an interesting reflection in the matter of the status of *vitrea* and *osceola*. In the former population (and assuming the two to be allopatric species), the jaw size increases from the farthest periphery toward the general direction of *osceola*, in the latter, the jaws decrease in size in going from Virginia south and west in the direction of *vitrea*. There is perhaps an even continuum of the 6-8 percent ratio between the populations of the Ozarks on one hand and west Florida on the other, which, if proved, would result in a great crescent ranging from North Dakota to southeastern Virginia, with the JL/HL ratio only 5 percent at one extreme, but increasing to 9 percent at the other.

Alabama and Mississippi, as well as Georgia, are thus the areas of primary significance in the eventual resolution of this problem. At least the first two States mentioned should also contain specimens the prostate glands of which are intermediate in size, if the two species here considered are actually only geographic races of a single, far-flung species.

The reproductive systems do not vary appreciably within the range here assigned to the nominal species *osceola*.

Summary of variability in several structural characters in the species of the Vitrea *group*

Dimension	*Vitrea*		*Osceola*	
	Mean	Range	Mean	Range
Body length (mm.)	2. 35	(1.91–2.62)	2. 34	(1.67–2.78)
Maximum diameter (mm.)	0. 41	(0.32–0.52)	0. 42	(0.34–0.60)
Head length (mm.)	0. 38	(0.32–0.48)	0. 41	(0.32–0.56)
Head diameter (mm.)	0. 26	(0.21–0.32)	0. 29	(0.25–0.36)
Sucker diameter (mm.)	0. 28	(0.20–0.34)	0. 30	(0.22–0.40)
Diameter of spermiducal gland at base (microns)	62	(44–72)	60	(46–80)
Diameter of prostate gland at base (microns)	50	(36–60)	33	(20–46)
Diameter of ental bulb of spermatheca (microns)	92	(70–140)	56	(32–80)
Jaw length divided by head length (%)	8. 1	(4.8–7.3)	8. 2	(7.2–8.8)

DISTRIBUTION.—From extreme southeastern Virginia south into the western panhandle of Florida, inferentially southward into the peninsular part of that State. This is a distributional pattern characteristic of a great many species of plants and animals, possibly developing as a consequence of (1) recession of the shore line during the Tertiary, and (2) the simultaneous dissection of the old Cretaceous peneplain of eastern North America with the destruction of lotic habitats in the interior. So far as collection data go, it appears that *osceola* is largely confined to various species of *Procambarus*, but its range is less extensive than that even of *P. blandingii* in eastern United States. Specimens have been examined from the following localities:

VIRGINIA: CHARLES CITY COUNTY: Roadside ditch about 1 mile south of Providence Forge on Va. Hy. 155, June 2, 1949, P. C. Holt and M. L. Bobb (PCH 226). ISLE OF WIGHT COUNTY: Roadside ditch 2.8 miles east of Franklin on U.S. Hy. 58, May 31, 1949, Holt and Bobb (PCH 220). NANSEMOND COUNTY: Along U.S. Hy. 58, just west of Suffolk, May 31, 1949, Holt and Bobb (PCH 221).

SOUTHAMPTON COUNTY: Nottoway Swamp, 3.8 miles east of Courtland on U.S. Hy. 58, May 31, 1948, Holt and Bobb (PCH 219).

NORTH CAROLINA: WILSON COUNTY: Saratoga, April 18, 1956, Horton H. Hobbs (PCH 733).

SOUTH CAROLINA: BARNWELL COUNTY: April 20, 1956, Hobbs (PCH 710). CALHOUN COUNTY: 2.9 miles north of the Orangeburg County line, April 20, 1956, Hobbs (PCH 708).

GEORGIA: DECATUR COUNTY: Tributary to Mosquito Creek, just north of Chattahoochee, Florida, on Ga. Hy. 97, September 9, 1955, Hobbs and Hart (PCH 662). SEMINOLE COUNTY: 3.1 miles north of Iron City, September 9, 1955, Hobbs and Hart (PCH 661).

FLORIDA: LEVY COUNTY: Southwest of Otter Creek, April 1948, Hobbs (PCH 163). CALHOUN COUNTY: 7.7 miles south of Altha, September 3, 1955, Hobbs and Hart (PCH 664).

In addition, the published records of Goodnight (1941) for Florida and Georgia, under the name *vitrea*, probably apply to this form, and may be provisionally accepted. These records extend the range somewhat farther south onto the Florida peninsula.

REMARKS.—This species is named for the Seminole Chief Osceola, a heroic leader of the resistance of his people during their conflict with the United States Government.

INGENS GROUP

The mountains of the southern Appalachian system are inhabited by a very large and distinctive *Cambarincola* which fully warrants segregation into a distinct group.

Cambarincola ingens seems specialized in the characters of size and very long prostate, but nonetheless shows primitive features in the prominent deferent lobes of the spermiducal gland and the relatively slightly differentiated cuboidal epithelium of the prostate. I would suspect that it, or its progenitor, separated from the main line of evolution in the Philadelphica section at a fairly early stage.

Cambarincola ingens, new species

FIGURES 3, 4, 33, 34

Cambarincola philadelphica (not Leidy, 1851) Ellis, 1919, Proc. U.S. Nat. Mus., vol. 55, p. 260 (in part, West Virginia records only).—Goodnight, 1943, Journ. Parasitology, vol. 29, p. 100 (in part, Virginia record only).

TYPE SPECIMENS.—Holotype, USNM 29944, from *Cambarus sciotensis* collected in Sinking Creek about 1 mile west of Newport, Giles County, Virginia, by Ben I. Johns, June 27, 1953. Topoparatypes from the same collection (PCH 499) and the following, both from the type locality: July 1947, Horton H. Hobbs and others (PCH 234), and July 3, 1950, Holt, Tuten, and Kizer (PCH 407).

DIAGNOSIS.—A very large species of *Cambarincola*, adults to 12 mm. long in life and up to 6 mm. after preservation; in which the prostate is much longer than the spermiducal gland, beyond the end of which it is slightly sinuous or even loosely coiled, with a prominent clear terminal bulb. Spermiducal gland with a distinct posterior deferent lobe. Jaws heteromorphic but about equal in size, the dorsal dental formula 3 or 5, the ventral 4.

DESCRIPTION.—A large robust worm with a rather large head, body fairly slender with gradually increasing diameter to segment VII; segments about twice as broad as long; prosomites not greater in diameter than the metasomites.

Head broad, of considerably greater diameter than segment I, its length about one-sixth the total length of the animal. Peristomium not distinctly set off by a basal constriction, somewhat produced forward, with four distinct lobations on the dorsal half and two broader ventral lobes.

Jaws massive, similar in both size and shape in lateral aspect, anisomorphic, the dental formula 1–2 or 3–4, often 5–4 in young specimens. Median tooth of dorsal jaw not appreciably larger than paramedian teeth of lower jaw.

Male reproductive system moderate in size. Bursa ovoid to subcordate in lateral aspect, equally divided internally between atrium and penial sheath; penis small, conical, not extending down into atrium when in repose. Ejaculatory duct of moderate length, enlarged near the middle where about one-third the bursa diameter, extending dorsad up to about the middle of the segment. Spermiducal gland cylindrical, slender, its diameter usually less then half that of the bursa, extending cephaloventrad below level of ental end of bursa, at which point a small but distinct posterior deferent lobe occurs, overhanging the region of the penial sheath. Prostate gland elongate, slender, its diameter consistently about two-thirds that of the spermiducal gland, which however it greatly exceeds in length, the portion which extends beyond the anterior deferent duct being reflexed upon itself and uniformly sinuous and spiraled in form, with a distinct clear terminal bulb. Histologically the prostate differs from the adjacent gland, but the cuboidal cells are proportionately not so large and well-formed as in species of the Philadelphica group.

Spermatheca extending dorsad about half-way up the segment, composed of a cylindrical, thick ectal duct and an ovoid enlarged ental bulb, these two regions about equal in length. No glandular ental process.

VARIATION.—Except in such ontogenetically changeable characters as body size and distinctness of the dentition, there appears to be no evident variation in this species as regards the major specific

characters. The male reproductive system agrees in both size and proportions among specimens from the northern and southern extremities of the known range. Sexually mature animals range in length (preserved) from 4.0 to 6.5 mm., indicating considerable continuation of growth following maturity.

AFFINITIES.—Insofar as genital characters are concerned, this species is obviously closest to members of the Philadelphica group. It shares part of its range with both *C. philadelphica* and *C. fallax*, resembling the former in jaw characters and the latter in the development of peristomial tentacles. Probably it is phylogenetically closest, among living species, to *C. philadelphica*, and a study of the isolating mechanisms operating where these two occur together would be a matter of some interest.

DISTRIBUTION.—The southern Appalachians, from western North Carolina to extreme southeastern West Virginia, in the Blue Ridge and Valley and Ridge physiographic provinces. Specimens have been examined from the following localities:

NORTH CAROLINA: ASHE COUNTY: Buffalo Creek near Jefferson, June 14, 1950, Horton H. Hobbs and C. W. Hart (PCH 343). MACON COUNTY: Small tributary to Leatherman Creek, about 8 miles northwest of Franklin, July 18, 1958, R. L. Hoffman (PCH 881). WATAUGA COUNTY: Winkler's Creek at Boone, June 21, 1948, Mike Wright (PCH 132); Valle Crucis, June 14, 1950, Hobbs and Hart (PCH 350).

TENNESSEE: CARTER COUNTY: Catbird Creek, Shenandoah Heights Park, Johnson City, January 3, 1954, Holt (PCH 579). JOHNSON COUNTY: Tenn. Hy. 91, 10.7 miles southwest of Damascus, May 27, 1951, Holt (PCH 589). UNICOI COUNTY: Sam's Creek, 3 miles south of Flagpond, July 7, 1951, Holt (PCH 452); Jones Branch, July 2, 1955, Holt (PCH 583).

VIRGINIA: CARROLL COUNTY: U.S. Hy. 221, 3.1 miles south of Woodlawn, June 13, 1950, Hobbs and Hart (PCH 328). FLOYD COUNTY: U.S. Hy. 221, 7.9 miles south of Floyd, June 13, 1950, Hobbs and Hart (PCH 325); Hy. 221, south of Willis, June 13, 1950, Hobbs and Hart (PCH 326). GILES COUNTY: Sinking Creek, 1 mile west of Newport, July 1947, Hobbs and others (PCH 234), July 3, 1950, Holt, Tuten, Kizer (PCH 407), June 27, 1953, B. L. Johns (PCH 499); Cascades of Little Stony Creek, July 1947, Hobbs (PCH 243), June 25, 1952 (PCH 492); Big Stony Creek, August 14, 1950, W. R. Whitehurst (PCH 411). GRAYSON COUNTY: Comer's Rock Recreation Area, July 16, 1949, Holt (PCH 257); pasture stream northeast of Buck Mountain, July 17, 1949, Holt (PCH 259); stream northeast of High Rock on Buck Mountain, July 17, 1949, Holt (PCH 261); tributary to Big Wilson Creek about 4 miles south of Mouth of Wilson on Va. Hy. 16, June 14, 1950, Hobbs and Hart (PCH 339). PATRICK COUNTY: Rock Castle Creek, west of Woolwine on Va. Hy. 8, July 5, 1947, Hobbs and Wilson (PCH 290). WASHINGTON COUNTY: Tributary to Middle Fork of Holston River, 10.6 miles northeast of Abingdon on U.S. Hy. 11, April 14, 1951, Hobbs and West (PCH 436). WYTHE COUNTY: Wytheville, no date given, M. M. McDonald (USNM 17698); Reed Creek, 3.3 miles southwest of Wytheville on U.S. Hy. 11, April 14, 1951, Hobbs and West (PCH 439).

WEST VIRGINIA: GREENBRIER COUNTY: Dry Creek near White Sulphur Springs, July 3, 1947, Hobbs (PCH 294). MERCER COUNTY: East River, 5.3 miles south-

west of Glen Lyn on U.S. Hy. 460, July 13, 1947, Hobbs and Wilson (PCH 109). SUMMERS COUNTY: Berger's Spring at Hinton, no date or collector given (USNM 17868). MONROE COUNTY: Indian Creek, August 6, 1900, U.S. Fish Commission (USNM 17691). County not determined: "Crane Creek," August 8, 1900, USFC (USNM 17687).

The range of this striking branchiobdellid does not correspond closely with that of any crayfish known to me, but is remarkably similar to that of *Desmognathus quadramaculatus*, a large plethodontid salamander with apparently similar ecological requirements. In Virginia and West Virginia, *Cambarincola ingens* seems largely restricted to the upper Kanawha drainage system, although spilling over (doubtless through recent stream captures) into the headwaters of both the Roanoke and Tennessee rivers. Further south, known localities are insufficient to invoke generalities, but the record for Macon County in western North Carolina suggests that *ingens* will eventually be found widespread as far as the mountains of Georgia. These Carolinian worms appear to be identical in sexual characters with others from Virginia, a specific homogeneity which provides little information about geographic variability but does permit the inference that *ingens* is continuously distributed over its range with little or no opportunities for local populations to become differentiated.

REMARKS.—That such an imposing species, abundant over its fairly extensive distribution, would be overlooked for so long is due in part to the traditional appeal to external characters in the definition of species. Specimens of *ingens* have been reported by Ellis (1919) under the name *philadelphica*, and I suspect that the material reported as that species from Reed Creek, Wythe [misspelled "Wortle"] County, Virginia, by Goodnight (1943) is likewise referable to *ingens* which is common in that stream.

Although collected from several species of crayfish, *ingens* seems most commonly to be found on *Cambarus sciotensis* Rhoades, which is by far the largest member of its genus in the upper Kanawha River system. Neither the crayfish nor the branchiobdellid have yet been taken in the adjacent headwater streams of the James River system.

The name *ingens* (Lat., huge) is given in consideration of the great size of this species, not approached by any other cambarincolid of eastern United States.

PHILADELPHICA GROUP

This is the trouble spot of the genus. To begin with, it contains the little-known and frequently misunderstood species *philadelphica* of Leidy, which is fairly widespread and variable in some respects. This variation, however, is not of the same nature as that which induced Ellis, and, following him, Goodnight, to make the species a

sort of catch-all. Actually the jaw structure and form of the sex organs is relatively stable, it is the individual and geographic variation in size, shape, peristomial lobation, and such characters which lend complications in the definition of specific limits. The heterogeneity of "philadelphica" in the sense of previous workers is here considerably abated by the extraction of a large element under the name *fallax*, a very distinctive and easily recognized form. Remaining are several stumbling blocks: The disposal of some rather distinctive subspecific populations now known to occur within the species, the relationship of *philadelphica* to *C. chirocephala*, and the status of *C. macrodonta* and *C. meyeri*. These matters are discussed more explicitly under the treatments of the respective entities.

The Philadelphica group is defined within the section by the relationship of prostate to spermiducal gland, viz, they are essentially subequal in length and collectively slightly curved and the prostate generally averages from one-half to two-thirds the diameter of the gland. There is no lobation (or but very little) of the gland at the entry of the deferent ducts. In general the group is definable on the basis of negative characters, including species not readily absorbed by the other three groups.

The male reproductive system remains remarkably similar in most of the species. There are a few deviants, such as the shortened prostate of *meyeri* and the reduced spermiducal gland of *chirocephala*, but in general such differences are only comparative. As a rule the jaws are dissimilar but equal in size except in *chirocephala*. An exception occurs in the new species *fallax*, which is homognathous with a 5–5 dental formula, and is placed in a separate subgroup. In most of the species the peristomium is divided into dorsal and ventral halves, with the dorsal produced into low but distinct blunt projections or even into elongate tentacles (again in *fallax*). Body form is variable, depending to some extent on the mode of preservation, but in a very general way the metasomites of *chirocephala* and *fallax* tend to be appreciably greater in diameter than the prosomites, imparting a strongly moniliform appearance to the outline of the body. The members of the group are here considered to be relatively closely related, separable largely by appeal to what I am inclined to consider characters of no great phylogenetic significance, yet fairly conspicuous and of the grade which has drawn the attention of most previous investigators.

Although the species themselves are not very difficult to define, their disposal into groups and subgroups has not been easy to accomplish, and the present arrangement represents only an arbitrary and subjective attempt. There seems to be little doubt that the male sex organs provide characters of the first order, but the necessity

has arisen of giving systematic supremacy to either peristomial configuration or jaw structure. As the latter is at least apparently fixed and invariable regardless of condition of the animal, I have made it the basis for recognition of a subgroup which contains two homognathous species, one with distinct peristomial tentacles, the other with a complete and entire peristomium.

A brief history of the described forms: The first member of this group to be named was called *Astacobdella philadelphica*, by Joseph Leidy in 1851. The description (the first validation of a name for an American branchiobdellid) was drawn largely from living specimens, and is fairly detailed. We can extract information on size, shape, peristomium, and jaw structure, and arrive at the impression of a worm which is essentially similar to recently acquired topotypical specimens from Philadelphica. In 1912, Max M. Ellis described specimens of a similar species from Colorado under the name *Cambarincola macrodonta*, making the separation largely on the basis of differences in the form of the peristomium—lobed or "crenulated" in *philadelphica* but entire in *macrodonta*.

Subsequently, in 1919, Ellis discussed variation in *philadelphica*, following the study of a considerable volume of material from his own collections in the midwest and those accumulated at the U.S. National Museum. Working with a much broader species concept than we now know to be justified, Ellis considered *philadelphica* to be a widespread, variable species, with the variation affecting both dental formula (in small details) and degree of lobation of the peristomium. Ellis believed that the normal lobes of the upper half of the peristomium could be extended or retracted at will by living animals, and that the size and shape of the lobes, varying from none to distinct tentacles, was likewise subject to the vagaries of preservation. Material identified as this species indicated a geographic range from New York to Wisconsin, and south to Kentucky and North Carolina (remarkably enough, almost identical with the present range of the species in its restricted sense).

In the same paper, Ellis described a species under the name *Cambarincola chirocephala*, based on specimens from Missouri in which peristomial lobes are present as in *philadelphica*, but the jaws unequal in size—the dorsal jaw from 1.5 to 2 times as wide as the ventral. In this paper, Ellis also published locality records for his species *macrodonta* from a number of widely scattered western states. Subsequent restudy of this material shows that Ellis has confused several species. Most of his specimens were either immature, overstained, or mounted flattened so that little more than the jaws could be seen.

No further attention was paid to this group of branchiobdellids until 1940, when there appeared the general monograph of the American species, by Clarence J. Goodnight. This paper is of interest to us at this point largely because of the remarkable treatment of the species of the Philadelphica group. In the case of *Cambarincola*, he recognized two subgenera, making the distinction by the following contrast:

> Upper lip composed of four subequal lobes. . . . *Coronata*, n. subg.
> Upper lip entire excepting a small median emargination.
> *Cambarincola*, n. subg.

According to Goodnight, the nominate subgenus consisted of the generotype species *macrodonta*, and *elevata* Goodnight, *vitrea* Ellis, and *inversa* Ellis. His new subgenus included the type *philadelphica* and *chirocephala* of Ellis. Curiously enough, this subgeneric dichotomy was proposed in defiance of a statement by Ellis which Goodnight then quoted under the treatment of *philadelphica:* "It was also found that worms of this species could flatten the entire lip, so that the lobes were scarcely visible." The virtue of Goodnight's groupings can be estimated by the fact that *macrodonta*, of one subgenus, can hardly be separated from the species of the other, while the nominate subgenus as originally proposed contained species which we now know to belong in three different genera. There is no defensible reason for continued recognition of the name *Coronata*, it is an absolute junior synonym of *Cambarincola* in the strictest sense.

Subsequent to 1940, one additional species has been named which is referable to the Philadelphica group. This is *Cambarincola meyeri* Goodnight, 1942, from central Kentucky.

The exact status of *C. okadai* Yamaguchi remains in great doubt. The species was described on the basis of worms taken from American crayfish introduced into Lake Chuzenji, near Nikko, Japan. The combination of tentaculated peristomium and homognathous, pentadont jaws strongly suggests that *okadai* is a senior synonym of the species here named *fallax*. The same combination, however, is found in the western *macrocephala*, and until more is known about the type material of *okadai*, or at least the origin of the crayfishes upon which it lived, we may continue to regard the species as *inquirendum*. Goodnight (1940, p. 41) dismissed *okadai* as probably based on specimens of *philadelphica*, ". . . as it differs from it only in the dentition of the lower jaw, and *C. philadelphica* is an extreme variable form as outlined above." The "above" referred to here is the quotation from Ellis's 1919 paper concerning variation in peristomial form only. Ellis did not consciously stretch variability in his *philadelphica* so far as to embrace two entirely different jaw shapes.

In the belief that *philadelphica* was both homognathous and heterognathous, tentaculate as well as not, Goodnight identified Virginia worms submitted to him in 1948 by P. C. Holt as typical of that species. On the basis of this information, Holt published in 1949 an account of the reproductive organs of the species, under the name *philadelphica*, although subsequent examination of his slides indicates that actually the material is mostly *fallax*. That a single species should encompass such variability, however, appeared unlikely to Holt, and he subsequently (1951) expressed some doubt about the correctness of Goodnight's determination in a discussion of worms from piedmont Virginia which had been named as *philadelphica*.

On the basis of a great number of specimens examined from numerous localities throughout the Appalachian region, I must conclude that jaw shape is a constant and reliable specific character, and is correlated with other structural specialties of a less conspicuous, but no less significant nature.

Two new species are herein added to the Philadelphica group, and there is every reason to assume that others will be disclosed by the future location of isolated endemic forms as well as by the analysis of more abundant material from eastern United States. The nominate species itself is almost certainly polytypic, as discussed in connection with the species. A number of variant forms in this general complex are omitted from present consideration, being known only from single specimens or poorly preserved material.

The following key to species should be approached like most keys—as an aid in identification rather than as the source of ultimate authority. Actually, this and other keys in the present paper are provided largely in order to give a tabular view of species grouped somewhat according to their presumed relationships. No key is as satisfactory as pictures when taxonomic characters are highly subjective ones!

Cambarincola meyeri is, with the utmost reluctance, entered as a member of both subgroups, owing to its poorly understood characters. See the discussion of this matter under the specific heading on page 355.

Key to Species of the Philadelphica Group

1. Homognathous species, the two jaws similar in size and shape, the median tooth always much larger than the laterals, dental formula 3–3 or 5–5 (FALLAX SUBGROUP) 2

   Heterognathous species, the jaws dissimilar in shape and often also in size; the dental formula 3–4, 5–4, 1–2, or a similar combination of odd (dorsal) and even (ventral) numbers of teeth (PHILADELPHICA SUBGROUP) . . . 4

2. Peristomium obviously tentaculate; prostate virtually as long as spermiducal gland (Appalachian Mountains and adjacent Piedmont areas from western New York to central Georgia) . . . . **Cambarincola fallax,** new species

   Peristomium entire or nearly so, no trace of lobes or tentacles 3

3. Prostate nearly as long as spermiducal gland; spermatheca long, slender, and not entally enlarged (western Virginia).

Cambarincola holostoma, new species

Prostate less than half as long as spermiducal gland; the latter unusually stout and strongly curved; spermatheca with a narrow ectal duct and large, subglobose ental bulb (Kentucky) . . **Cambarincola meyeri** Goodnight

4. Peristomium at least with four blunt lobes on its dorsal half; dorsal jaw generally at least somewhat longer and larger than the ventral 5

Peristomium at the most divided into dorsal and ventral halves, the dorsal without lobes; jaws essentially subequal in size at least in lateral aspect . 6

5. Head relatively larger (fig. 43), dorsal jaw distinctly broader than ventral (fig. 44); spermiducal gland comparatively small with respect to the prostate (central eastern Kentucky and Indiana west through the Ozark region into Kansas and Oklahoma, the diagnostic characters becoming accentuated westwardly) . . . . . **Cambarincola chirocephala** Ellis

Head relatively smaller (fig. 39), dorsal jaw only slightly broader than ventral (fig. 40); spermiducal gland relatively large in comparison with the prostate (North Carolina and Tennessee north to New York, west in the Great Lakes region to Wisconsin). **Cambarincola philadelphica** (Leidy)

6. Prostate gland at least half as long as spermiducal gland, usually subequal in length; latter elongated, slender, not recurved (fig. 38); spermatheca with a long ectal neck and a moderate ental bulb (western margin of the Great Plains in Colorado and adjacent states).

Cambarincola macrodonta Ellis

Prostate less than half as long as the stout, recurved spermiducal gland; spermatheca with a very short ectal duct and a large, globose ental bulb (Kentucky) . . . . . **Cambarincola meyeri** Goodnight

Cambarincola philadelphica (Leidy)

FIGURES 39–42, 51–54, 57

Astacobdella philadelphica Leidy, 1851, Proc. Acad. Nat. Sci. Philadelphia, 1851, p. 209.—Verrill, 1873, Rep. U.S. Fish. Comm. for 1872–1873, p. 688 (name only).

Branchiobdella philadelphica Moore, 1893, Proc. Acad. Nat. Sci. Philadelphia, vol. 45, p. 427.

Bdellodrilus philadelphicus Moore, 1895, Journ. Morphology, vol. 10, p. 497; 1901, Bull. Illinois State Lab. Nat. Hist., no. 5, p. 542.—Pierantoni, 1912, Ann. Mus. Zool. Univ. Napoli, new ser., vol. 3, no. 24, p. 17.

Cambarincola philadelphica Ellis, 1912, Proc. U.S. Nat. Mus., vol. 42, p. 484.—Hall, 1914, Proc. U.S. Nat. Mus., vol. 48, p. 190.—Ellis, 1918, Trans. American Microsc. Soc., vol. 37, p. 49; 1919, Proc. U.S. Nat. Mus., vol. 55, p. 260.—Goodnight, 1939, Journ. Parasitology, vol. 25, supp., p. 11 (abstract); 1940, Rep. Reelfoot Lake Biol. Station, vol. 4, p. 171 (New York records); 1940, Illinois Biol. Monogr., vol. 17, no. 3, p. 38 (records for N.C., Pa., W. Va., probably this species).—Holt, 1954, Virginia Journ. Sci., new ser., vol. 5, p. 169.—Holt and Hoffman, 1959, Journ. Tennessee Acad. Sci., vol. 34, p. 103.

Cambarincola philadelphia (sic) Yamaguchi, 1933, Proc. Imp. Acad. vol. 9, p. 191.

[The following references almost certainly pertain to other species]:

Cambarincola philadelphica Goodnight, 1941, Trans. American Microsc. Soc., vol. 60, p. 70 (Florida records); 1943, Journ. Parasitology, vol. 29, p. 100

(Virginia and Missouri records).—Rioja, 1943, Anal. Inst. Biol. (Mexico), vol. 14, p. 544 (Mexican records).

TYPE SPECIMENS.—Present whereabouts unknown. Originally from crayfish—probably *Cambarus bartonii*—collected by Joseph Leidy in streams in and around Philadelphia, Pennsylvania. Topotypes (PCH 695) from Wissahickon Creek in Philadelphia have been studied.

DIAGNOSIS.—A medium to large-sized, variable species of the Philadelphica group, characterized by the following combination of characters (only well-preserved specimens, in series, can be determined with certainty): Peristomium divided into dorsal and ventral halves, the dorsal larger and with four low marginal lobations; jaws relatively large and subrectangular in lateral aspect, the dorsal jaw usually a little larger than the ventral; male reproductive system moderate in size, filling from half to two-thirds of the coelom of one side of segment VI; bursa elongate, at least twice as long as broad, the penial sheath merging gradually into a fairly short ejaculatory duct; spermiducal gland slender and recurved ventrad, twice the diameter of prostate, latter long and slender, reaching to ental end of spermiducal gland.

DESCRIPTION (from "typical" northeastern specimens).—Body moderate to large in size, maximum length 5.0 mm. Proportions about normal for the genus, but anterior part of body less attenuated than in most species; segments IV to VIII of about equal diameter; prosomites about three times length of metasomites and of greater diameter, at least on anteriormost segments; caudal sucker small, its diameter less than that of segment I.

Head fairly large, as long as first three body segments, and its diameter equal to that of segment II; largest basally, narrowing slightly to base of peristomium which is set off by a distinct constriction and divided into two subequal halves. Dorsal half somewhat larger and longer than the ventral, and provided along its margin with four low rounded lobes (not visible in poorly preserved specimens, either macerated or shrunken), the ventral half with a median incision dividing it into two broad lobes. Peristomium not or but very slightly flared, generally continuing the head profile in lateral aspect.

Jaws massive, anisomorphic, heterodont, the dental formula 5–4 or 3–4, sometimes 3–2 in old specimens; dorsal jaw slightly larger than ventral, both, in lateral aspect, almost as high as long and thus subrectangular in appearance. Median tooth of dorsal jaw and paramedians of ventral larger than the lateral cusps but not to the extent seen in such species as *fallax*, *chirocephala*, and others.

Male reproductive system variable in size, usually occupying from one-half to two-thirds of the coelom of one side of the segment. Bursa typically elongate, at least twice as long as wide, most of the length being contributed by the atrium; penial sheath of normal

size and proportions and confined to the ental third of the bursa. Ejaculatory duct broadest ectally, merging gradually into penial sheath; entally it becomes narrower and is rather short in total length. Spermiducal gland long and slender, curving cephalad and then abruptly ventrad, extending down as far as level of penial sheath, frequently with a small fairly distinct posterior deferent lobe visible near the ental end. Prostate long and slender, half the diameter of the spermiducal gland or less, but extending ventrad to the level of the ental end of the latter, with a small but distinct terminal bulb.

Spermatheca without specific peculiarities, consisting of the slender, elongate ectal duct extending about one-third the way up one side, a fusiform ental bulb, and a distinct, fairly large glandular ental process.

VARIATION.—The allegedly great variability of what has been identified under the name *philadelphica* has become almost legendary. Ellis (1919) gave the idea its momentum in remarking that material from Douglas Lake, Michigan, occasionally has a dental formula higher than the usual 5–4 (presumably 7–4 or 7–6), and that the lobation of the peristomium was to some extent a function of their extension or contraction at the time of death. Now these remarks are perfectly in order, reflecting nothing more than one might expect in the line of individual and ontogenetic variation, but Ellis concluded by saying "*Cambarincola philadelphica* was the most variable species studied," and his words like those of many another pioneer were misused by his followers.

We now know that Ellis unfortunately mixed several species under his concept of *philadelphica*, including *mesochorea* and *fallax*. But his concluding statement was picked up by Goodnight and even used out of context to justify the relegation of *C. okadai* to the synonymy of *philadelphica*.

The foregoing preamble is not meant to deny variability within the limits of *philadelphica*, but to indicate that previous ideas on this score had little factual basis.

In the large amount of material available, I found that the species here identified as *philadelphica* is a rather plastic and complicated ensemble of microraces and incipient subspecies. Owing in part, at least, to differences in the way the crayfish hosts were preserved, there is a dismaying range in the size, shape, and proportions involved. However, in the most general terms, one can recognize fairly well-defined populations on the basis of body form, these to be mentioned in their turn. There is little appreciable difference in the reproductive systems, notably some variation in the overall size of the male organs which in some scattered localities tend to occupy more of the coelomic cavity than is typical for the species. Whether this reflects the

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condition at maturity or some stage in the sexual activity, some sort of allometric growth, or merely sporadic local variation cannot be established at this time. The situation seems to be restricted to the southern Appalachian region.

There is considerable, apparently geographic, variation in size and shape of the jaws. The attention of future workers is particularly invited to investigation of this matter, something which I have been unable to do satisfactorily.

As diagnosed and briefly described in the preceding paragraphs, *philadelphica* ranges from central New York State west as far as

FIGURES 39–42.—Structural details of *Cambarincola philadelphica* (Leidy). 39, Lateral aspect of typical specimen; 40, jaws of the same specimen, dorsolateral aspect; 41, jaws of another specimen, lateral aspect; 42, reproductive systems, specimen from Frederick Co., Maryland.

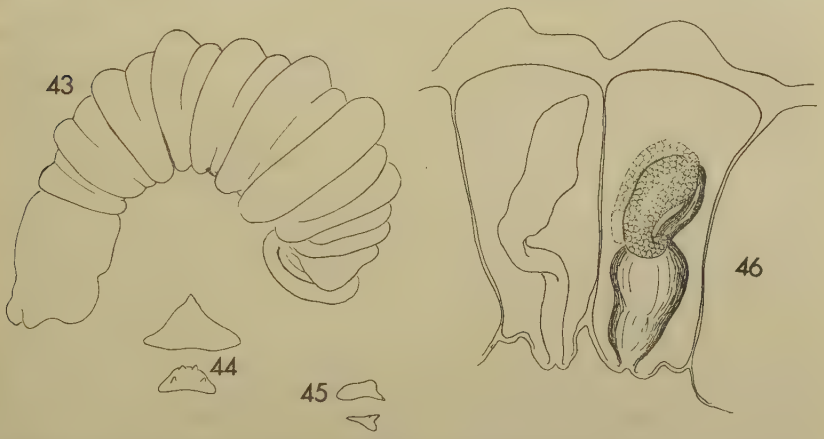
Minnesota, and south through the Appalachians and Piedmont to the Carolinas. An additional form appears to inhabit the Catskill region and adjacent areas, this is generally similar to the typical form but is apparently consistently smaller over a distinct geographic range. At several localities it occurs together with the large *philadelphica*. Whether it represents (1) a depauperate northern phase of the main population, (2) a distinct sibling species, or (3) merely an assemblage of young specimens, remains to be worked out by another investigator able to collect and make field studies in New York.

In central Kentucky and Tennessee occurs a form in which the peristomium, particularly the dorsal half, is hypertrophied and frequently widely flared, giving the head a campanulate appearance. This is probably a perfectly good subspecies, but the details of its overlap with *philadelphica* in eastern Kentucky ought to be worked

out prior to a formal recognition. The problem is complicated by the nearby occurrence of *chirocephala* which also appears to intergrade with *philadelphica*.

Representative specimens of each of the three forms of this species are illustrated, and material is separated appropriately in the lists of specimens examined. There is little or no appreciable difference in the reproductive systems.

Affinities.—The species of the Philadelphica subgroup are all closely related and by no means easy to separate. A complication is introduced by the certainty that additional forms will be discovered and defined, particularly in the Appalachian region. Of the named



Figures 43–46.—Structural details of *Cambarincola chirocephala* Ellis. 43, Lateral aspect of typical specimen, Benton Co., Arkansas; 44, dorsal aspect of jaws, specimen from Benton Co., Arkansas; 45, lateral aspect of jaws, specimen from Logan Co., Arkansas; 46, lateral aspect of reproductive systems, specimen from Logan Co., Arkansas.

forms, *philadelphica*, *chirocephala*, and *macrodonta* are most alike, and future work may indeed show them to be only components of a wide-ranging polytypic species. Some of the Kentucky material listed under *chirocephala* shows a remarkable similarity in almost every respect to *philadelphica*, and I have been able to demonstrate gradual east-west clinal variation in both the jaws and spermiducal gland of *chirocephala*. That these two species intergrade seems almost certain. Perhaps the establishment of an arbitrary ratio of jaw widths will help define the ranges of the two, as well as their intermediates.

The relationships of *philadelphica* to *macrodonta* are also very close. The entire peristomium of the latter is a good distinction between well-preserved material of the two, and if present impressions are correct, the smaller bursa (less than the spermiducal gland in diameter) of *macrodonta* should aid in recognition of the species. *C. macrodonta* apparently occurs in South Dakota, *philadelphica* in Wisconsin.

Obviously the northern part of the Mississippi Valley is an area of some importance in establishing whether or not these two species overlap or intergrade.

DISTRIBUTION.—Northeastern United States, from New York west to Wisconsin, south through the Appalachian system as far as South Carolina and Tennessee. Material of the typical form of the species has been seen from the following collections:

MARYLAND: FREDERICK COUNTY: Catoctin Creek between Brunswick and Point of Rocks on Md. Hy. 464, October 12, 1952, L. B. Holthuis (PCH 600).

MINNESOTA: WRIGHT COUNTY: Clearwater River at Minn. Hy. 152, in the town of Clearwater, July 20, 1958, Holt (PCH 790).

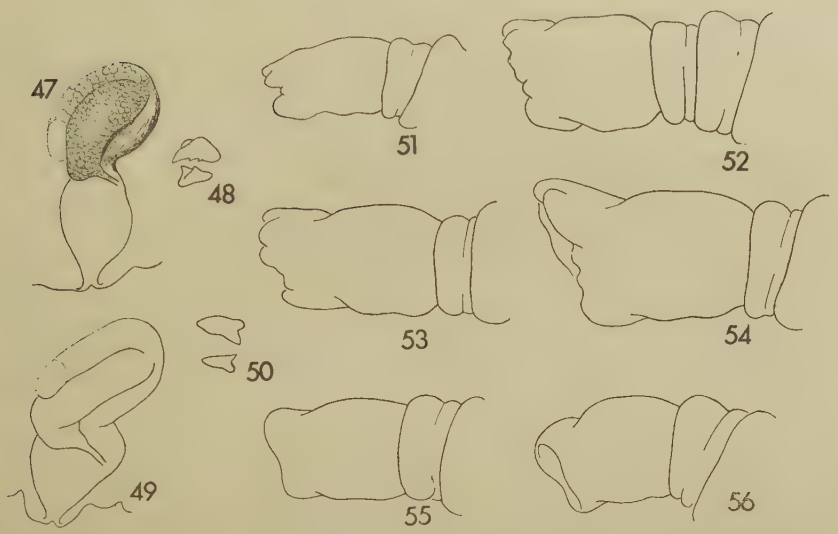
NORTH CAROLINA: WATAUGA COUNTY: Campus pond at Boone, June 24, 1948, Mike Wright (PCH 128).

NEW YORK: FRANKLIN COUNTY: Chateauguay River just west of Chateauguay on U.S. Hy. 11, May 21, 1951, D. W. Crocker and A. Gustafson (PCH 634). LEWIS COUNTY: Mohawk River at West Leyden, August 22, 1952, Crocker (PCH 552); outlet of Brantingham Lake, 3.5 miles north of Lyons Falls, May 21, 1951, Crocker and Gustafson, (PCH 639). TIOGA COUNTY: Catatonk Creek at Candor, August 29, 1952, Crocker (PCH 569). TOMPKINS COUNTY: Owasco Inlet, 3 miles south of Groton, May 18, 1951, E. C. Raney (PCH 628). WYOMING COUNTY: Cattaragus Creek at Arcada, August 29, 1952, Crocker (PCH 570).

PENNSYLVANIA: PHILADELPHIA COUNTY: Wissahickon Creek in Philadelphia, September 2, 1957, C. W. Hart (PCH 695).

SOUTH CAROLINA: YORK COUNTY: 4.0 miles south of Rock Hill on S.C. Hy. 72, April 20, 1958, Holt (PCH 748).

VIRGINIA: ALLEGHANY COUNTY: Dolly Ann Creek, 2 miles east of Covington on U.S. Hy. 60, June 18, 1948, G. Ailstock (PCH 115). AMHERST COUNTY: Pedlar River, 6.3 miles northwest of Forks of Buffalo on U.S. Hy. 60, November 11, 1947, Horton H. Hobbs (PCH 82). AUGUSTA COUNTY: 7.6 miles north of Steeles Tavern on U.S. Hy. 11, May 11, 1947, Hobbs (PCH 71). BEDFORD COUNTY: Little Otter River, 3.1 miles east of Bedford on U.S. Hy. 460, Holt and Bobb (PCH 73). BRUNSWICK COUNTY: 2.9 miles north of Edgerton on Va. Hy. 140, May 31, 1949, Holt and Bobb (PCH 217). BUCKINGHAM COUNTY: 9.6 miles south of Sprouse's Corners on U.S. Hy. 15, November 9, 1946, Hobbs and Hoffman (PCH 36). CAMPBELL COUNTY: Evington, July 13, 1947, Hobbs (PCH 106). CRAIG COUNTY: 1.5 miles south of Paint Bank on Va. Hy. 311, June 24, 1948, Hobbs (PCH 97). CHESTERFIELD COUNTY: Small stream below the lake in Camp Shawandasee, near Chesterfield Courthouse, May 14, 1949, Holt (PCH 211). FLUVANNA COUNTY: 1.5 miles south of Palmyra on U.S. Hy. 15, November 10, 1946, Hobbs and Hoffman (PCH 114). GRAYSON COUNTY: Stream in pasture north of High Rock, northwest of Independence, July 17, 1949, Holt (PCH 260). HANOVER COUNTY: 3.1 miles north of Ashland on U.S. Hy. 1, June 3, 1949, Holt and Bobb (PCH 230). HIGHLAND COUNTY: Shaw's Creek, 6.6 miles east of McDowell on U.S. Hy. 250, September 27, 1946, Hobbs (PCH 113). LOUISA COUNTY: 25.5 miles east of Charlottesville on U.S. Hy. 250, July 2, 1948, Holt and Bobb (PCH 121). MONTGOMERY COUNTY: Trillium Dale at Blacksburg, November 17, 1957, Holt, Riggin, Hoffman (PCH 873); Bottom Creek, 0.5 mile northeast of Otey on Va. Hy. 637, May 22, 1958, Holt and Hoffman (PCH 874). NELSON COUNTY: North Fork of Rockfish River, 5.4 miles south of Afton on Va. Hy. 151, September 1, 1946, Hobbs (PCH 112). ROCKBRIDGE COUNTY: Tributary to Buffalo Creek, 5.3 miles south of Lexington on U.S. Hy. 11, May 11, 1947, Hobbs (PCH 75); 4.3



FIGURES 47–56.—Structural details of three species of *Cambarincola*. 47–50, *C. chirocephala:* 47, Male reproductive system, Carroll Co., Arkansas; 48, jaws, caudolateral aspect, same specimen; 49, male reproductive system, Parke Co., Indiana; 50, jaws, lateral aspect, same specimen. 51–54, *C. philadelphica*, heads in lateral aspect: 51, Small northern form, Tompkins Co., New York; 52, typical form, Montgomery Co., Virginia; 53, amplistomate form, Jackson Co., Kentucky; 54, amplistomate form, Macon Co., North Carolina. 55, 56, *C. macrodonta:* paratypes, Boulder Co., Colorado, both specimens show the characteristic entire peristomium.

miles north of Glasgow on U.S. Hy. 501, May 11, 1947, Hobbs (PCH 78). ROCKINGHAM COUNTY: Swift Run, 3 miles east of Elkton, December 12, 1946, Holt (PCH 14). SCOTT COUNTY: Troublesome Creek, 8.2 miles west of Gate City on U.S. Hy. 58, June 16, 1950, Hobbs and Hart (PCH 366).

WEST VIRGINIA: East River, date and collector not stated (USNM 17705) [probably in Mercer County, southwest of Glen Lyn].

Specimens of the small New York phase (either a depauperate form of *philadelphica* or possibly a different species) have been examined from the following collections:

NEW YORK: CHENANGO COUNTY: Otego Creek, just east of Oneonta, August 27, 1952, Crocker (PCH 561). ONEIDA COUNTY: Tributary to the N.Y. State Barge Canal just west of Utica, August 23, 1952, Crocker (PCH 536); Oswego River at Rome, August 22, 1952, Crocker (PCH 583). TIOGA COUNTY: Catatonk Creek at Candor, September 6, 1959, L. R. McManus (PCH 928). TOMPKINS COUNTY: Owasco Inlet, 3 miles south of Groton, May 18, 1951, E. C. Raney (PCH 628). WARREN COUNTY: Stony Creek, in the town of Stony Creek, August 19, 1952, Crocker (PCH 546).

Material of the form with enlarged peristomium, discussed in the foregoing text, has been examined from the following localities:

KENTUCKY: JACKSON COUNTY: 1.8 miles south of Bond, July 29, 1958, Holt (PCH 831). WOLFE COUNTY: 1.7 miles west of Compton on Ky. Hy. 15, July 31,

1958, Holt, (PCH 846); large stream 5.1 miles east of Compton on Ky. Hy. 15, July 31, 1958, Holt (PCH 847).

North Carolina: macon county: Spillway of Lake Ravenel, Highlands, July 8–15, 1958, Hoffman (PCH 875); Buck Creek drainage 3.5 miles northwest of Highlands, August 3, 1958, Hoffman (PCH 884).

Tennessee: cumberland county: White Creek, 0.25 mile northwest of Alloway, May 3, 1959, Holt and Ford (PCH 903).

Cambarincola chirocephala Ellis

Figures 43–50, 57

Cambarincola chirocephala Ellis, 1919, Proc. U.S. Nat. Mus., vol. 55, p. 263, figs. 18, 19.—Goodnight, 1940, Illinois Biol. Monogr., vol. 17, no. 3, p. 37 (in part, Ill., Ind., Ky., Mo., ?Ala. records); 1940, Rep. Reelfoot Lake Biol. Station, vol. 4, p. 171 (?Tenn. record).—Holt and Hoffman, 1959, Journ. Tennessee Acad. Sci. vol. 34, p. 103.

Type specimen.—Holotype, USNM 17713, from *Orconectes virilis* collected at Rolla, Phelps County, Missouri, by J. Barley. This specimen is mounted flattened dorsoventrally, showing the jaws clearly; the reproductive systems are obscured.

Diagnosis.—A small member of the Philadelphica group, recognized by the distinctly disparate anisomorphic jaws; by the reduced size of the spermiducal gland and prostate (both often shorter than the bursa); and by the elongate, slender, gradually enlarged spermatheca.

Description.—Body small, ranging from 1.5 to 2.5 mm. in length, the greatest diameter at segment vii; prosomites of all segments larger than metasomites. Diameter of segment i less than that of head; segments ix and x reduced, the caudal sucker abruptly enlarged, equaling or surpassing diameter of head.

Head of normal size and form for the genus, larger than segment i, as long as the first three body segments combined. Peristomium conspicuously set off by a basal constriction, flared, its margin provided with four small lobes on the dorsal side and two broad, lower lobes on the ventral.

Jaws disparate in both dorsal and lateral aspects, anisomorphic; broadly triangular. Dorsal jaw largest, 1.5 to 2 times as broad as the ventral, the median tooth very conspicuous, lateral cusps small or obscure. Ventral jaw subtrapezoid, with two small paramedian apical teeth and a median sinus, and a smaller sublateral cusp on each side halfway to the base.

Male reproductive system moderate in size, extending dorsal through about three-fourths of segment vi. Bursa elongate, pyriform, 2 or 3 times as long as its greatest diameter, the latter more than half the length of the ventral part of the segment. Atrial portion of bursa somewhat longer than the penial sheath. Ejaculatory duct long and slender, two-thirds to three-fourths as long as the

FIGURE 57.—Distribution of the three species of the Philadelphica subgroup. ○, *C. philadelphica;* ⊙, "amplistomate" variety of *philadelphica;* ◑, *C. macrodonta;* ●, *C. chirocephala.*

bursa, subequal in length to the prostate gland. Spermiducal gland relatively small, subequal to or shorter than length of bursa, its ental end recurved caudomesad prior to entry of the anterior deferent duct. Prostate relatively large, nearly as long and thick as spermiducal gland, the terminal bulb large and conspicuous.

Spermatheca long and slender, the ectal half curving laterad around the gut, ental half more or less abruptly enlarged to 1.5 to 2 times the diameter of ectal portion, the apex bluntly acuminate, not set off as an evident ental process. Total length of spermatheca somewhat greater than diameter of segment VII.

VARIATION.—Individual variation in this species is very slight, involving chiefly differences in size of the body. The proportions of the reproductive tracts remain constant for a given locality.

There is, however, some evidence that the sexual organs are subject to the influence of geographic factors affecting variation. There appears to be an east to west decrease in the spermiducal gland length as indicated by the illustrations (figs. 47, 49). In Indiana

and Kentucky material, this organ is fairly robust and somewhat longer than the bursa, while in specimens from Arkansas it is reduced in overall size and is shorter than the bursal length. The prostate remains unaffected over this range, so that in the southwest it becomes porportionately longer and broader with respect to the spermiducal gland. Presumably this variation is of at least potential systematic interest, but whether it is evenly clinal in nature, or broken at some intermediate area (such as the Mississippi River) cannot be ascertained on the basis of available material. Specimens from Illinois are presently not at hand for study, and for the time being the matter must rest at this point.

There appears to be a similar east to west cline in jaw structure, with the disparity in size becoming most distinct westward into Kansas and Oklahoma. Kentucky material tentatively referred to *chirocephala* can scarcely be distinguished from *philadelphica* on the basis of size of the jaws.

DISTRIBUTION.—*Cambarincola chirocephala* appears to be basically autochthonous to the Ozark highlands, now reaching its greatest abundance in northern Arkansas and Missouri. It extends, however, eastward into Indiana and Kentucky where its range meets that of *philadelphica*, with which it perhaps intergrades. Most of the Indiana localities are in the Wabash River system; one, interestingly enough, is in the Maumee River system which now drains northeast into Lake Erie. The presence of *chirocephala* in this drainage reflects either fairly recent stream piracy in the region or transgression of the low divides by crayfish—either possibility seeming equally likely. It will be a matter of interest to establish additional records for the species in northwestern Ohio and eastern Indiana. Goodnight (1940, p. 38) has reported this species from a number of midwestern localities as well as from some very unlikely stations in New York and Virginia, and such extralimital records must be presumed to have been based upon misidentifications.

MATERIAL EXAMINED: 22 slides, from the following localities:

ARKANSAS: BENTON COUNTY: Sugar Creek at crossing of U.S. Hy. 62, July 6, 1958, Holt (PCH 768). CARROLL COUNTY: South Fork of Dry Creek, 2.8 miles east of Green Forest on U.S. Hy. 62, July 6, 1958, Holt (PCH 766). CRITTENDEN COUNTY: 14.6 miles south of Marked Tree on U.S. Hy. 63, July 5, 1958, Holt (PCH 758). FULTON COUNTY: Salem, July 29, 1941, Horton H. Hobbs (PCH 310). LOGAN COUNTY: West fork of Mill Creek, 4.4 miles west of Delaware on Ark. Hy. 22, July 30, 1941, Hobbs (PCH 189). NEWTON COUNTY: Buffalo River, 14 miles south of Harrison on Ark. Hy. 7, July 29, 1941, Hobbs (PCH 175). SHARP COUNTY: 3.2 miles southeast of Hardy, July 29, 1941, Hobbs (PCH 176); about 9 miles west of Hardy, July 6, 1958, Holt (PCH 760).

INDIANA: ALLEN COUNTY: St. Mary's River at Fort Wayne, Max M. Ellis (USNM 17706). MONROE COUNTY: Bloomington, May 1915, Will Scott (USNM

17709). PARKE COUNTY: 5.6 miles west of Bellmore on U.S. Hy. 36, July 26, 1958, Holt (PCH 807).

KANSAS: HARPER COUNTY: 10.7 miles west of the county line on Kans. Hy. 14, July 8, 1958, Holt (PCH 776).

KENTUCKY: CLARK COUNTY: 9.7 miles east of Winchester on Ky. Hy. 15, July 30, 1958, Holt (PCH 839). JACKSON COUNTY: 0.1 mile south of the Owsley County line on Ky. Hy. 30, July 29, 1958, Holt (PCH 834). MADISON COUNTY: Otter Creek, 9.3 miles north of Richmond on U.S. Hy. 227, July 30, 1958, Holt (PCH 841). OWSLEY COUNTY: Traveler's Rest, July 29, 1958, Holt (PCH 835). POWELL COUNTY: 1.4 miles east of Slade on Ky. Hys. 11 and 13; also Natural Bridge State Park, both July 29, 1958, Holt (PCH 836, 837).

MISSOURI: PHELPS COUNTY: Rolla, J. Barley (USNM 17713, the holotype). WASHINGTON COUNTY: Irondale, August 28, 1931, Robert Rice (PCH 168).

OKLAHOMA: COMANCHE COUNTY: Blue Beaver Creek in Fort Sill, June 6, 1959, J. W. Berry (PCH 905).

TENNESSEE: HUMPHREYS COUNTY: Hurricane Creek, 10.2 miles east of Waverly on U.S. Hy. 70, July 5, 1958, Holt (PCH 756).

REMARKS.—Goodnight (1940, p. 37) has emphasized the pronounced elevation of prosomites over metasomites as diagnostic of the species, and most specimens are so formed, but contracted individuals of many branchiobdellids likewise assume a distinctly annulated appearance. The larger size of the dorsal jaw is a good character for recognition of *chirocephala* over most of its range, but it must be recalled that in Kentucky this character loses must of its significance.

The affinities of *chirocephala* are discussed in connection with *C. philadelphica;* in brief, the likelihood of a genetic continuum between the two seems good. However, the actual details of this relationship are not clear at this time. Whether *chirocephala* represents the fairly recent modification of a westwardly migrating *philadelphica*-stock or whether it is an allopatrically differentiating species now radiating from its place of origin and intergrading with the original parent population remains to be established.

The name *chirocephala* (Gk. *chiros*, hand, and *cephalos*, head) presumably refers to the dorsal lobation of the peristomium, but it is not particularly appropriate since none of the material examined is more distinctly lobed than most specimens of even *C. philadelphica*, and in no way approximates the conspicuous tentaculation of *fallax* and some other species. Ellis himself misidentified the Indiana material cited as *philadelphica*, the records being originally published in the same paper as the description of *chirocephala!* The Indiana worms were merely mounted in such a way that the jaws could not be seen in dorsal aspect.

Cambarincola macrodonta Ellis

FIGURES 37, 38, 55, 56, 57

Cambarincola macrodonta Ellis, 1912, Proc. U.S. Nat. Mus., vol. 42, p. 481, figs. 1–3; 1919, Proc. U.S. Nat. Mus., vol. 55, p. 257 (Colorado records only?).—

Hall, 1914, Proc. U.S. Nat. Mus., vol. 48, p. 190.—Goodnight, 1940, Illinois Biol. Monogr., vol. 17, no. 3, p. 31 (description only); 1940, Rep. Reelfoot Lake Biol. Station, vol. 4, p. 171 (?South Dakota record).—Holt and Hoffman, 1959, Journ. Tennessee Acad. Sci., vol. 34, p. 97, figs. 1–6 (redescription of species).

TYPE SPECIMENS.—Holotype and two paratypes, USNM 53794, from *Cambarus diogenes* collected at Boulder, Boulder County, Colorado, by Max M. Ellis.

DIAGNOSIS.—A moderately small member of the genus, differing from other members of the Philadelphica group by the combination of the slender, elongate outline of both body and head, the large anisomorphic subequal jaws; entire peristomial margin; relatively large bursa in comparison with the long, slender spermiducal gland, and shortened prostate gland. The ectal spermathecal duct is much longer in relation to size of the ental bulb than in the other related species.

DESCRIPTION.—A distinctly slender and graceful worm, the body only slightly thicker at maximum diameter than at the narrowest part, tapering more distinctly caudally down to the small caudal sucker, its diameter less than that of either head or segment I. Segments less than twice as long as broad, the length almost equally divided into prosomite and metasomite, the former not at all larger in diameter than the latter.

Head rather long and narrow, about equal to first three segments combined, its greatest diameter a little greater than that of segment I. Peristomium set off by a basal constriction, not evidently flared, the margin divided into dorsal and ventral halves but neither half with lobes or tentacles.

Jaws large and massive, subtriangular in dorsal aspect, anisomorphic, heterodont, the dental formula 5–4; dorsal jaw slightly larger than ventral in lateral aspect, its median tooth subequal to the paramedian teeth of the ventral jaw.

Male reproductive system of moderate size, occupying half of one side of the coelom of segment VI or less, the bursa elongate pyriform, its greatest diameter near the ental third instead of near the midlength as in related forms; ejaculatory duct short, about equal to bursal diameter. Spermiducal gland slender and elongate, oriented almost horizontally in striking contrast to the oblique dorsoventral position taken by the gland in most other related species, increasing slightly in diameter entally, with the ental fourth of the length bent a little ventrad. Deferent lobes small or absent. Prostate about two-thirds as long as spermiducal gland and from one-fourth to one-half its diameter, extending along the dorsal side entally about as far as the entry of the posterior deferent duct.

Spermatheca composed of three parts: An elongate, slender, muscular walled ectal duct, which extends about halfway up the side of segment v; a subglobose or ovoid ental bulb; and a small terminal ental process composed of glandular cells.

Variation.—The material which was studied from three localities in Colorado is relatively homogeneous as regards structure of the jaws and reproductive systems, variations in these details being largely a reflection of difference in size of the worms. It is quite true that branchiobdellids are very variable in size after maturity, suggesting continuous growth through life, and actual measurements carry less significance than ratios of the measurements.

Various combinations of measurements as functions of some standard have been plotted graphically, and most of these show that the material of *macrodonta* examined maintains a very constant set of proportions despite changes in overall size. One suggestive detail involves relative head size. Three specimens from Fort Collins, Colorado, yield a head diameter to body diameter ratio of .60, .61, and .62. In eleven other specimens from Boulder and Black Wolf Creek, Colorado, the same ratio ranges from .71 to .99, with an average of .83. These values, plotted along the horizontal axis of a chart with body-length intervals on the vertical axis, separate out into two discrete groups. Unfortunately, it cannot be ascertained whether we are dealing here with true geographic variation or with the effects of preservation. Within a fairly wide latitude, the degree of contraction or distention of a branchiobdellid after preservation is influenced by the strength of the alcohol used. The foregoing example is introduced to remark the likelihood that with uniformly preserved worms in good series, a future student of the group will be able to cope with the problems inherent in the study of soft-bodied, muscular animals.

Affinities.—*Cambarincola macrodonta* is without doubt closely related to *C. philadelphica*, and if the two occurred as sympatric or adjacent allopatric forms, it would be difficult to separate them with confidence. In well-preserved specimens, the peristomial character is most useful, but some individuals of *philadelphica* often do not show the peristomial lobes, and it is easy to understand how various other species have been misidentified by previous workers as *macrodonta*. On the basis of my own limited knowledge of the species, I would judge it to be an isolated, conservative remnant of the old late Tertiary pre-*philadelphica* stock which has become isolated in the foothills of the Rockies by recent climatic events which have produced the now semiarid nature of the Great Plains.

Distribution.—This species has been recorded from 12 States ranging from New Mexico to Virginia, from South Dakota to Louisiana. The specimens which I have been able to re-examine, those identified

by Ellis in the U.S. National Museum collection, fall into three categories: Very small, obviously immature worms; adult but misidentified specimens; and, finally, a few slides of worms conspecific with the type specimen. The juveniles are at present unidentifiable with certainty. Misidentified adults include *C. mesochorea* and some other species which cannot be confidently identified but which are not *macrodonta* on jaw shape. Undoubted specimens of the species are listed as follows:

COLORADO: BOULDER COUNTY: Boulder, September 1915, Max M. Ellis (USNM 17667). LARIMER COUNTY: Fort Collins, L. C. Bragg (USNM 17662). YUMA COUNTY: Black Wolf Creek, near Beecher's Island, October 1915, B. Jaffa (USNM 17664).

In addition to these Colorado records, the specimen cited by Ellis from Las Vegas, New Mexico (USNM 17661), appears to be a *macrodonta*, but is so heavily stained that the sex organs cannot be seen. There is nothing from a geographic point of view to preclude the specimen being *macrodonta*.

Specimens from Muldon and Agricultural College, Mississippi, are very much like Colorado material in every respect, yet I hesitate to admit them to the list of *macrodonta* localities, at least until more material from Mississippi or from intermediate areas comes to hand.

Cambarincola meyeri Goodnight

FIGURES 67, 68

Cambarincola meyeri Goodnight, 1942, Trans. American Microsc. Soc., vol. 61, no. 3, p. 272, figs. 1–3.—Holt and Hoffman, 1959, Journ. Tennessee Acad. Sci., vol. 34, p. 103.

TYPE SPECIMEN.—Holotype, USNM 20597, from *Cambarus bartonii* collected in Raven's Creek, near Lexington, Fayette County, Kentucky, by Marvin C. Meyer (date unknown).

DIAGNOSIS.—A small to moderate-sized member of the Philadelphica group characterized particularly by the (?) entire peristomium, stout reniform spermiducal gland with a short slender prostate, and peculiar form of the spermatheca.

DESCRIPTION.—Length of holotype about 3.5 mm. Body of normal proportions, segmental diameter about three times the length at midbody; segments IV–VI of essentially the same size; prosomites elevated above level of metasomites; caudal sucker quite small, its diameter less than that of head or of segment I.

Head of moderate size, as long as first three body segments and slightly wider than segment I. Peristomium set off by a basal constriction, slightly flared but the margin entire except for being divided into a dorsal and ventral half; no evidence of lobes visible.

Jaws fairly small for size of head, heteromorphic, the dorsal jaw with a large median tooth and two very small cusps at its base on each side; ventral jaw with two large paramedian teeth and a single small cusp at the outer base of each. Jaws virtually identical in size, the dorsal very slightly wider at the base.

Male reproductive system characterized by the small globose bursa (its diameter less than that of the spermiducal gland), by the very slender, tubular prostate which is less than half as long as the spermiducal gland, and by the stout, acutely reniform shape of the latter, its ental half curved strongly caudad and accentuating the region of the posterior deferent duct.

Spermatheca composed of three major portions: 1, An enlarged, muscular ectal region about half as large as the bursa; 2, a strongly constricted cervical region of the ectal duct; and 3, a greatly expanded, thin-walled, subglobose ental bulb.

Variation.—The species is known only from two specimens. Goodnight's original description must have been based upon the paratype which he retained, for the holotype is somewhat larger than the published dimensions, its dorsal jaw 0.11 mm. in width instead of 0.07 as stated by Goodnight for his specimen. Having studied but the single specimen, I cannot say anything further on the subject of variation.

Affinities.—*C. meyeri* is undoubtedly a member of the Philadelphica subgroup, but differs from the others at least in the slender, short prostate and strongly curved, heavy spermiducal gland. It is possible that Goodnight's observation on the peristomium will be confirmed, to constitute another diagnostic feature. Had no specimens been available for study, my inclination would have been to dismiss the name as probably a junior synonym of *philadelphica* or one of its localized races.

Goodnight states that "*Cambarincola meyeri* is closely related to *Cambarincola vitrea* Ellis, but differs in the structure of the upper jaw." I agree to a relationship between the two, but only as members of the same genus; actually they seem to be very dissimilar and fall into different groups of the Philadelphica section.

Distribution.—Known definitely only from the type locality.

Remarks.—The status of this species is by no means as well-established as might be desired. I have at hand a large series of well-preserved specimens from the vicinity of Livingston, Overton County, Tennessee (Holt, leg.), which agree in virtually every detail with the holotype of *meyeri*, not only in size and shape of the body, but also in small details of the reproductive systems. The concordance is such that conspecificity with the type specimen is almost assured. Yet there appears to be a discrepancy in the jaw struc-

ture—isomorphic and bipentadont in the Tennessee worms, anisomorphic and pentatetradont in *meyeri*. Two likelihoods can be considered: 1, The original types of *meyeri* may have been composite. Goodnight's account of the jaws was based on the paratype. Unfortunately, the dentition cannot be made out with certainty in the holotype, owing to its orientation on the slide; 2, the types of *meyeri* may be aberrant specimens with respect to jaw structure, if we assume that both are anisomorphic.

The question is one which can be settled only by the study of a series of fresh specimens from the type locality. On the basis of present knowledge of the group, it seems utterly unlikely that virtual identity in form of the sex organs would be contraverted by a basic difference in jaw structure.

For the present, however, I refrain from identifying the Tennessee worms as *meyeri*, remarking only their great similarity to the type of that species, and commending the matter to someone having the opportunity to secure topotypes of the species.

Cambarincola fallax, new species

FIGURES 58–60, 62, 63

Cambarincola philadelphica (in part) Ellis, 1919, Proc. U.S. Nat. Mus., vol. 55, p. 262.—Goodnight, 1940, Illinois Biol. Monogr., vol. 17, no. 3, p. 38.—Holt, 1949, Journ. Morphology, vol. 84, p. 535 et seq.

?*Cambarincola okadai* Yamaguchi, 1933, Proc. Imp. Acad., vol. 9, no. 4, p. 191; 1934, Journ. Fac. Sci. Hokkaido Imp. Univ., vol. 3, no. 3, p. 190.

TYPE SPECIMENS.—Holotype and four paratypes, USNM 29945, from *Cambarus longulus* subsp. collected in Maiden Spring Creek, about 1 mile east of Wardell, Tazewell County, Virginia, on June 19, 1959, by R. L. Hoffman. Additional paratypes from the same collection, PCH 904.

DIAGNOSIS.—A moderate to large species of the Philadelphica group characterized by the combination of homognathous, pentadont jaws and conspicuous elongate peristomial tentacles.

DESCRIPTION.—A moderate to fairly large species, up to about 4.0 mm. in length. Body form rather slender, without distinct enlargement in diameter in going caudad to the middle of the length. Prosomites about twice as long as metasomites and very distinctly larger in diameter, imparting a pronounced annulate body profile. Segments II to VII usually of about equal diameter.

Head moderate in size, about as long as first three body segments combined, its diameter about equal to that of segment II, equal to or slightly larger than diameter of caudal sucker. Peristomium large, set off by a deep basal constriction, almost half the total head length; the dorsal half often a little flared, with four distinct blunt

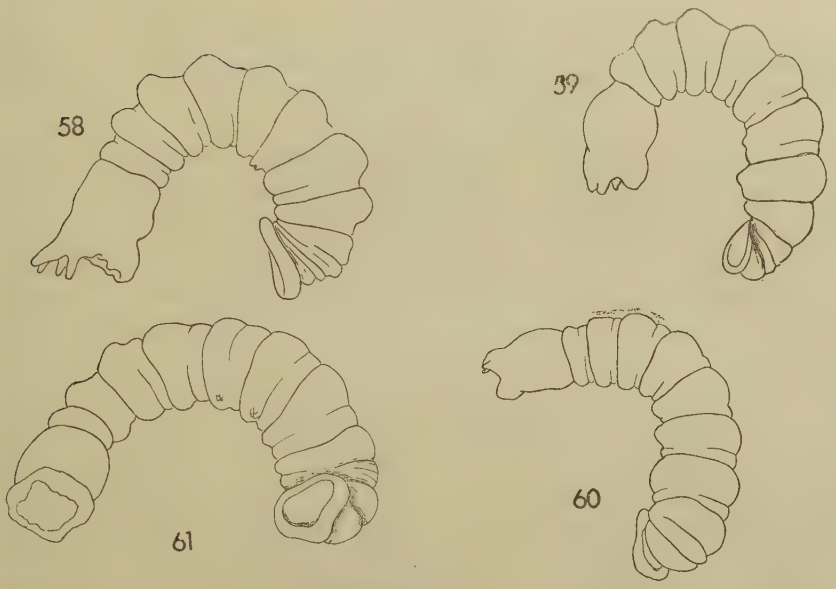


FIGURE 58–61.—Two species of the Fallax subgroup, external appearance. 58, *Cambarincola fallax*, new species, paratype from Tazewell Co., Virginia, with peristomium extended; 59, specimen from Seneca Lake, New York; 60, specimen from Pike Co., Georgia. 61, *C. holostoma*, new species, paratype from Highland Co., Virginia, showing the characteristic entire peristomium.

elongate tentacles of varying length. Ventral half of peristomium shorter, set off from dorsal by a deep lateral sinus each side, subdivided into two broad lobes.

Jaws about 10 percent of the head length, isomorphic, equal in size, heterodont; the median teeth distinctly larger than the lateral cusps which are nonetheless very distinct even in lateral aspect, dental formula 5–5, 5–3, or 3–3, the smaller figures occurring chiefly in old or large specimens.

Male reproductive system typical for the group, the more ectal organs of moderate size and occupying about two-thirds or less of the coelom on one side of segment VI. Bursa elongate pyriform, its greatest diameter at midlength; penial sheath abruptly merging into the much narrower ejaculatory duct; latter half as long as bursa. Spermiducal gland oriented almost dorsoventrally, extending down to or beyond level of penial sheath, generally subreniform in outline with an occasional enlargement homologous to the posterior deferent lobe of other species; diameter of gland about equal to that of bursa, but somewhat smaller in occasional specimens. Prostate gland long, slender, its diameter half that of spermiducal gland near their juncture; not extending entally as far as apex of the latter.

Spermatheca rather small, generally similar to that of *C. philadelphica*, composed of a slender ectal duct and an ovoid or fusiform ental bulb located about halfway up one side of segment v, no glandular ental process detected.

VARIATION.—Individual variation in body form and peristomial shape is shown in figures 58–60. The two most similar worms are from opposite extremes of the range.

The male reproductive system varies somewhat more than in most other members of this genus, particularly with respect to size of the spermiducal gland, but nothing has been noted to indicate any sort of geographic dispersion. Figure 62 shows the typical proportions of the larger organs. The spermatheca is likewise somewhat variable, particularly the appearance of the ental bulb. This, however, is pretty clearly a reflection of the degree of distention by its contents.

DISTRIBUTION.—Known from numerous localities throughout the Appalachian uplift and adjacent Piedmont from western New York south as far as central western Georgia. In the southern part of the range *fallax* appears to be the most abundant member of the genus, further north the records are more scattered and *C. philadelphica* becomes dominant. Material has been examined from the following localities:

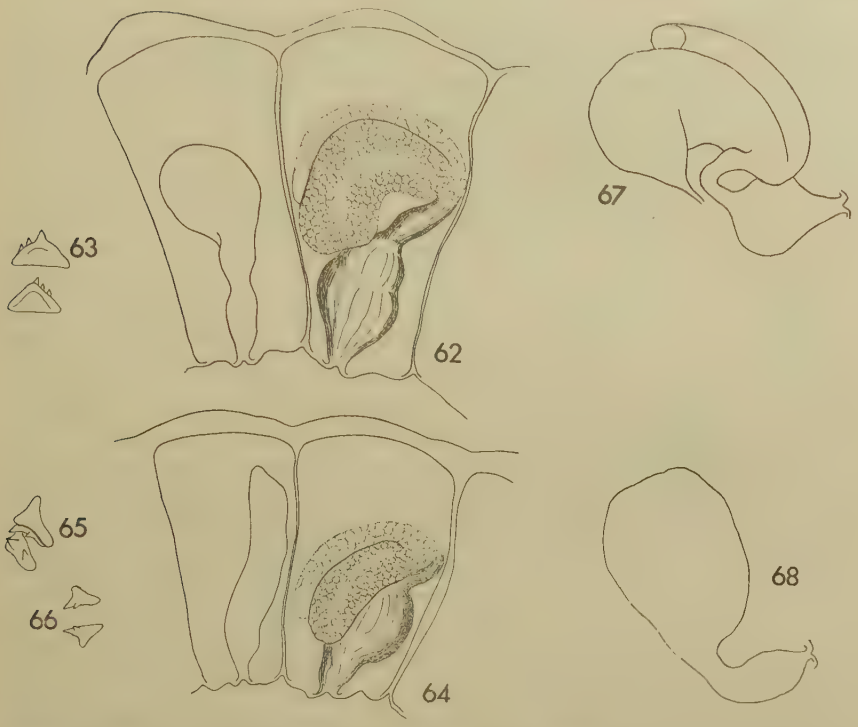
GEORGIA: FANNIN COUNTY: 5.7 miles south of Morganton on Ga. Hy. 60, November 6, 1958, K. Simonds (PCH 909). MURRAY COUNTY: Holly Creek, 10.6 miles north of the Gordon County line on U.S. Hy. 411, April 16, 1958, Holt (PCH 737). PIKE COUNTY: Large stream on outskirts of Zebulon, April 17, 1958, Holt (PCH 740). WHITE COUNTY: Small ravine, 1 mile south of Helen, July 11, 1958, Hoffman (PCH 877).

NORTH CAROLINA: CHEROKEE COUNTY: Beaver Creek, 0.5 mile northwest of Andrews, June 9, 1959, Simonds (PCH 912). CLAY COUNTY: 3 miles south of Tuni Gap on the Hayesville-Andrews road, June 5, 1959, Simonds (PCH 918).

TENNESSEE: MONROE COUNTY: Small woodland stream, 7 miles north of Madisonville on U.S. Hy. 411, April 16, 1958, Holt (PCH 738). POLK COUNTY: 2.3 miles south of Ocoee on U.S. Hy. 411, June 9, 1959, Simonds (PCH 907).

VIRGINIA: ALBEMARLE COUNTY: Tributary to Rivanna River near Stony Point, April 25, 1947, Holt and Hobbs (PCH 45, 46). BUCKINGHAM COUNTY: 9.6 miles south of Sprouses Corners on Va. Hy. 15, November 9, 1946, Hobbs and Hoffman (PCH 36). CHARLOTTE COUNTY: 8.8 miles south of Keysville on Va. Hy. 15, November 9, 1946, Hobbs and Hoffman (PCH 38). GILES COUNTY: Sinking Creek at Va. Hy. 700, near Newport, July 3, 1950, Holt, Tuten, and Kizer (PCH 407). PATRICK COUNTY: Shooting Creek, 1.6 miles south of the Franklin County line on Va. Hy. 40, April 13, 1953, Hobbs (PCH 723). TAZEWELL COUNTY: Maiden Spring Creek, about 1 mile east of Wardell, June 19, 1959, Hoffman (PCH 904, type series).

NEW YORK: TOMPKINS COUNTY: Owasco Inlet, 3 miles south of Groton, May 18, 1951, E. C. Raney (PCH 628). County not located: Reeder's Creek, 1949, L. C. Goldstein (PCH 245).



FIGURES 62–68.—Structural details of three species of *Cambarincola*. 62, *C. fallax*, new species, reproductive systems, specimen from Giles Co., Virginia; 63, dorsal aspect of jaws, same specimen, each jaw tilted slightly in opposite directions, dental formula actually 5–5. 64, *C. holostoma*, new species, reproductive systems, paratype from Highland Co., Virginia; 65, the same, jaws in dorsolateral aspect, same locality; 66, the same, jaws in lateral aspect, same locality. 67, *C. meyeri* Goodnight, male reproductive system, from holotype, Fayette Co., Kentucky; 68, the same, spermatheca from holotype, the specimen considerably flattened in mounting.

In addition to the foregoing records, there are doubtless many published localities for *C. philadelphica* which really apply to this species.

Cambarincola holostoma, new species

FIGURES 61, 64–66

TYPE SPECIMENS.—Holotype and four paratypes, USNM 29946, from *Cambarus bartonii* and *C. longulus* collected in Crab Run, 4 miles west of McDowell, Highland County, Virginia, on U.S. Hy. 250, by L. B. Holthuis, October 25, 1952. Topoparatypes, PCH 599.

DIAGNOSIS.—A member of the Fallax subgroup characterized by the long, slender body, the prosomites of which are not distinctly raised; by the completely entire, flared peristomium; and by the slender, elongate, fusiform spermatheca.

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DESCRIPTION.—A small worm reaching a maximum length of about 2.0 mm. in preserved specimens. Body form slender, the diameter increasing gradually to segment VI which is subequal in bulk to segments VII and VIII; caudal sucker somewhat larger than preceding segment and about as broad as the peristomium. Prosomites up to three times as long as the metasomites, but not of greater diameter.

Head about as long as the first three body segments combined, and equal in diameter to segment III, the peristomium set off by a very strong basal constriction and distinctly flared, its margin entire, without any trace of division into dorsal and ventral halves or into smaller lobes. Head otherwise not visibly segmented externally.

Jaws similar, dental formula 3–3 with the median tooth long and acute, the general appearance very similar to the jaws of *C. fallax* but the formula perhaps more often 3–3 than in that species.

Male reproductive system basically similar to that of other species of the Philadelphica group. Bursa rather long, equaling the length of the spermiducal gland, the two subequal in diameter. Ejaculatory duct modest in size, its length less than the diameter of the spermiducal gland. Latter of normal proportions, without evident lobation at entry of deferent ducts. Prostate long, slender, about half the diameter of spermiducal gland, which it joins slightly entally of the entry of the ejaculatory duct.

Spermatheca slender and elongate, curving laterad and dorsad around the gut, and becoming slightly wider but maintaining about the same diameter almost to its end at a point near the middorsal area of the segment, a distinct ental bulb not being well-developed.

VARIATION.—In the small amount of material examined from three localities, some of it not well-preserved, there appeared to be little or no variation in the diagnostic characters of the species.

AFFINITIES.—The relationships of this form with *C. fallax* and *C. philadelphica*, with both of which it is sympatric, are unquestionable. It differs from both, however, in characters of the peristomium and spermatheca. Closer relationship with *fallax* is postulated on the basis of jaw form, here considered to be a more fundamental character than peristomial lobation.

DISTRIBUTION.—Aside from the type locality, this species is known from two collections from western Virginia, in the James and upper Potomac River drainages.

VIRGINIA: CRAIG COUNTY: 1.5 miles south of Paint Bank on Va. Hy. 311, June 24, 1948, Horton H. Hobbs (PCH 97). ROCKINGHAM COUNTY: Swift Run, 3 miles east of Elkton on U.S. Hy. 33, December 12, 1946, Holt (PCH 14).

REMARKS.—Further knowledge of the distribution of this localized form may be of interest in providing an insight into the factors influencing its speciation.

FIGURES 69–73.—Structural details of two species of *Cambarincola*. 69, *C. heterognatha*, new species, paratype in lateral aspect; 70, the same, lateral aspect of jaws; 71, the same, reproductive systems. 72, *C. demissa*, new species, body profile of paratype, Wise Co., Virginia. Part of body wall shown cut away to indicate the size of the reduced reproductive organs in situ; 73, the same, reproductive systems in lateral aspect, same specimen.

The collection localities, all of which I have seen, are rather small, swift, mountain brooks, somewhat different in character from the larger and perhaps more placid streams in which *fallax* occurs most abundantly. Conceivably the peristomium of *holostoma* represents the development of (or retention of) a more efficient holdfast device than the dissected and lobed mouth of *fallax*, a matter which would certainly enhance the origin and maintainence of specific differences by ecological factors.

The problem is recommended to someone having the opportunity to study branchiobdellids and their distribution in the upper James River system of western Virginia.

HETEROGNATHA GROUP

A separate group must be erected to represent on a coordinate standing the very unusual and highly specialized new species described

below. In many of its structural features, such as the disparate jaw size and shape, small body, reduced size of the male reproductive system, and particularly the shortened prostate gland, this species shows a combination of evolutionary specialities which occur only singly in various other forms of the genus.

Cambarincola heterognatha, new species

FIGURES 69–71, 74

TYPE SPECIMENS.—Holotype and paratype, USNM 29947, from *Cambarus* sp. collected in a tributary to Big Wilson Creek, 4 miles south of Mouth of Wilson on Va. Hy. 16, Grayson County, Virginia, by Horton H. Hobbs, Jr., and C. W. Hart, June 14, 1950. Additional paratypes indicated in the list of specimens examined.

DIAGNOSIS.—Immediately recognizable by the remarkably dissimilar jaws alone. In addition, the male reproductive system is reduced in size and the prostate gland is less than half the length of the spermiducal gland.

DESCRIPTION.—A moderate-sized species, body length up to about 3.0 mm., somewhat fusiform in body outline, the greatest diameter at segments VI and VII, the least at X.

Head of normal size and proportions, about as broad as long, its diameter less than that of segment I; peristomium only a little flared, without marginal lobes; head indistinctly subdivided into two halves by a slightly median constriction. Jaws very dissimilar in size, the upper triangular with a large median projection and about eight times the bulk of the lower (!) which is about equally quadrate in shape with two small paramedian cusps.

Body outline fusiform, segments VI and VII largest, each somite divided by a distinct complete constriction, the prosomites the larger of the two subsegments and not, or only slightly, elevated over the level of the metasomites.

Male reproductive system rather small, extending only halfway up the side of segment VI. Bursa fusiform, widest near the middle, about 1.5 times as long as broad, somewhat constricted at entry of ejaculatory duct. Latter of moderate length and rather slender, less than a third the bursa diameter. Spermiducal gland subreniform, slightly broader entally, its diameter equal to or slightly greater than that of bursa, the length a little greater. Prostate small and slender, less than half as long as spermiducal gland, generally about a third as long, the terminal bulb distinct.

Spermatheca elongate and slender, abruptly constricted at the midlength, the ental half with a rounded tip or a slight ental process, the organ extending dorsad nearly to the dorsal side of the coelomic cavity.

FIGURE 74.—Distribution of *Cambarincola heterognatha*, new species, an abundant Appalachian endemic species. Each spot represents collections for one county.

VARIATION.—There is little or no appreciable variation in this species as regards size of body, shape of jaws, and general details of the sex organs. There is some individual divergence in the relative length of the prostate gland, which may vary anywhere from a third to half the length of the spermiducal gland, irrespective of locality. The single collection from Kentucky is interesting in that the prostate of all specimens studied is basally much thicker than noted elsewhere in the range of the species, attaining a diameter at its base at least half that of the spermiducal gland. The Kentucky locality is considerably removed from the main distribution of the species, and this minor difference may reflect some significant microevolutionary development due to isolation. Aside from this one departure, *heterognatha* must be considered a very homogeneous species despite its considerable geographic range.

DISTRIBUTION.—The southern Appalachians, from northwestern Virginia and adjacent West Virginia, south and west to central eastern parts of Tennessee and Kentucky. Specimens have been examined from the following localities:

KENTUCKY: ADAIR COUNTY: 8.9 miles east of Columbia on Ky. Hy. 80, July 28, 1958, Holt (PCH 827).

TENNESSEE: CLAIBORNE COUNTY: 3 miles southwest of New Tazewell on Tenn. Hy. 33, April 16, 1951, Horton H. Hobbs and W. R. West (PCH 540). CUMBERLAND COUNTY: Daddy's Creek, between Crossville and Pikeville, August 1950, Holt (PCH 419). WASHINGTON COUNTY: Hartsell Cove, Buffalo Mountain,

August 1953, Holt (PCH 495); Sinking Creek in Horse Cove, January 10, 1954, Holt (PCH 580).

North Carolina: watauga county: 2 miles south of Vilas on N.C. Hy. 194, June 14, 1950, Hobbs and Hart (PCH 350).

Virginia: augusta county: South River, 2.4 miles south of Waynesboro, September 3, 1948, Hobbs (PCH 271). craig county: 1.4 miles west of Newcastle on Va. Hy. 311, June 23, 1948, Hobbs (PCH 99). franklin county: Smart View Picnic Area, Blue Ridge Parkway, September 14, 1958, Holt and Hoffman (PCH 891). giles county: Cascades of Little Stony Creek, June 25, 1952, Holt (PCH 492, paratypes). grayson county: Tributary to Big Wilson Creek, 4 miles south of Mouth of Wilson, June 14, 1950, Hobbs and Hart (PCH 339, types). lee county: Hardy Creek, 11.1 miles west of Jonesville on U.S. Hy. 58, June 16, 1950, Hobbs and Hart (PCH 371). rockingham county: Swift Run, 3 miles east of Elkton, December 1946, Holt (PCH 4). smyth county: White Top Mountain, September 5, 1951, John T. Wood (PCH 531). tazewell county: Bluestone River, 11.2 miles northeast of Tazewell on U.S. Hy. 460, June 18, 1950, Hobbs and Hart (PCH 393, paratypes); Burkes Garden, June 30, 1947, R. L. Hoffman and H. I. Kleinpeter (PCH 532); Maiden Spring Creek, 1 mile east of Wardell, June 19, 1959, Hoffman (PCH 904). washington county: 9.5 miles south of Abingdon on U.S. Hy. 11, April 14, 1951, Hobbs and West (PCH 432); 4.8 miles south of Abingdon, April 14, 1951, Hobbs and West (PCH 435); North Bristol, January 1, 1954, W. A. Whittaker (PCH 581). wythe county: Reed Creek, 3.3 miles southwest of Wytheville on U.S. Hy. 11, April 14, 1951, Hobbs and West (PCH 439).

West Virginia: greenbrier county: Dry Creek, east side of Kates Mountain at White Sulphur Springs, July 3, 1947, Hobbs (PCH 294). pendleton county: 5.8 miles east of Franklin on U.S. Hy. 33, July 30, 1949, Hobbs and Word (PCH 275). wyoming county: Barker Creek, 5.3 miles south of Tralee, July 12, 1947, Hobbs and Wilson (PCH 95).

From the standpoint of major drainage systems, the vast majority of the preceding records lie within the basins of the upper Tennessee and Kanawha rivers, and southwest Virginia clearly seems to be the center of abundance for this species. Peripherally, the records are distinctly more spotty, although in equally well-collected areas. Towards the northeast, the species occurs in the James and Potomac drainage systems.

The single known locality for Kentucky lies in a region which was intensively collected by Dr. Holt during July 1958, a fact which permits the inference that *heterognatha* may exist in central Kentucky only as a relict, and this fact, together with the generally sporadic distribution of species suggests that the range may be in the process of contraction, perhaps as a result of post-Pleistocene increase in temperature in the southern Appalachians.

Nonetheless, it must be emphasized that the distribution of *heterognatha* is by no means well-known, and many new localities doubtless remain to be established.

Remarks.—It has already been observed that *heterognatha* is endowed with a remarkable combination of presumably evolutionary specializations. It is one of the easiest of branchiobdellids to recog-

nize, owing to the enormous dorsal jaw which dominates the entire anterior half of the head. In no other known form in the family is heterognathy carried to such an extreme.

Additionally, the spermatheca offers very good specific characters, particularly its length and pronounced median constriction which are evident in every specimen examined.

Presumably *heterognatha* is a highly modified member of the general *philadelphica-chirocephala* stock, which began to evolve its characters at a very remote time, or has been able to develop them more rapidly than other species of the genus.

DEMISSA SECTION

A separate section seems necessary to reflect the status of *Cambarincola demissa*, a very disjunct species which has little relationship with other members of the genus.

Judged from body shape, small head and jaws, and general appearance, this species is perhaps one modified as a gill-inhabiting form, and therefore especially liable to various structural concomittances of a specialized habitat. Unfortunately, we know nothing definite about the preferred microhabitat of the species.

Perhaps the most unusual feature of this animal is the marked reduction in the size of the reproductive systems, indicated in outline in the habit sketch of an entire worm (fig. 72). All of the normal organs are present, with the fine structure characteristic of the genus, but both spermiducal and prostate glands are very small proportionately, and the latter—although histologically not differentiated—terminates in a small clear bulb. The penial sheath of the bursa is much smaller, in relation to the atrium, than in any other member of the genus.

DEMISSA GROUP

A monotypic group with the characters of the section. The only species is a moderately small, corpulent-looking worm, probably branchiophilus, known only from extreme southwestern Virginia.

Cambarincola demissa, new species

FIGURES 72, 73

TYPE SPECIMENS.—Holotype and four paratypes, USNM 29948, from *Orconectes erichsonianus* and *O. juvenilis* collected in a tributary to the Powell River at Big Stone Gap, Wise County, Virginia, by Horton H. Hobbs, Jr., and C. W. Hart on June 17, 1950.

DIAGNOSIS.—A moderate-sized (2.8–3.2 mm. long) cuneate species of *Cambarincola*, differing from all other members of the genus in the exceptionally small sex organs, the prostate gland likewise differing

from all others in terminating in a small clear bulb although not histologically differentiated from the spermiducal gland.

DESCRIPTION.—Body strongly enlarged caudally, segments VI and VII about twice as wide as segment I, and tapering very abruptly to the fairly large caudal sucker which is as broad as the head or segment I. Segments very short, as little as a third of the body diameter at segment VI; prosomites twice as long as metasomites but not elevated above them.

Head as long as first three body segments, but smaller in diameter and thus continuing the anterior attenuation of the body; peristomium about a third of total head length, set off by a strong basal constriction, its margin apparently broadly lobed but not extended into projections or tentacles (all material slightly macerated). An additional more posterior constriction of the head occurs and imparts a trisegmented appearance to the head in lateral aspect.

Jaws relatively quite small, about 7.0 percent of the head length, the dorsal jaw slightly the larger and longer, with a distinct large projecting median tooth; ventral jaw likewise with a median tooth and subsimilar in general form to the dorsal, at least in lateral aspect (none of the available material is mounted in a way to show dorsal or ventral surfaces of the jaws, but careful observation indicates that the dental formula is probably 3–3 or perhaps even 1–1).

Male reproductive system very small, confined to the ventrolateral portion of the coelom of segment VI, extending dorsal less than halfway up one side of the segment. Bursa small, cordate, the atrial portion making up most of its bulk, the penial sheath confined to the ental fourth of the bursa and very small by comparison with that in other species. Ejaculatory duct moderately long, its length about equal to that of the bursa or spermiducal gland, its wall muscular but of normal thickness. Spermiducal gland and prostate collectively only about as large as the bursa, their histological structure similar (small, glandular, basophilic cells), but the prostate terminates in a small clear bulb presumably homologous to that so characteristic of the Philadelphica section. Spermiducal gland short and broad, at most only half again as long as the diameter; prostate slender but much shorter than spermiducal gland. Latter entally rounded, without evident lobation at the entries of the small, slender deferent ducts.

Spermathecae equally reduced, extending less than halfway up one side of segment V, the shape somewhat fusiform, expanding laterally from the small ectal portion and maintaining essentially the same size to the abruptly acuminate ental tip.

VARIATION.—Owing to the small amount of available material, all of which is slightly macerated from the initial preservation in weak alcohol, it is not possible to dwell at any length on the observed varia-

tion. Because of the small size of the sex organs, which are not particularly confined by the gut as in most other species, the spermiducal gland and prostate in particular are liable to considerable freedom of motion in the coelom, and preserved specimens show much variation in the shape of these two structures due to a difference in perspective. The spermatheca seems to have a constant shape, as does the general body outline. The range of this species may be so limited that geographically influenced variability will be found negligible.

Relationships.—There is no other species in the genus with which *demissa* can be compared. *C. branchiophila* of the Mesochorea section is known to be a gill form, and has small jaws and a cuneate body form, but its sex organs are of normal size and the major parts of the bursa correctly proportioned. It is difficult to derive *demissa* from either of the other two major sections of the genus, although if compelled to make a choice I should tentatively place it much closer to the Mesochorea section as representing the culmination of evolutionary tendencies in that ensemble. As this form is probably localized among the high mountains of southwest Virginia, there is every reason to presume that many other endemic species remain to be discovered, and some of these may cast some light on the affinities of this curious and disjunct little worm.

Distribution.—Aside from the type locality, *C. demissa* is known only from the following locality:

Virginia: tazewell county: Bluestone River, 11.2 miles east of Tazewell on U.S. Hy. 460; June 18, 1950, Hobbs and Hart (PCH 393).

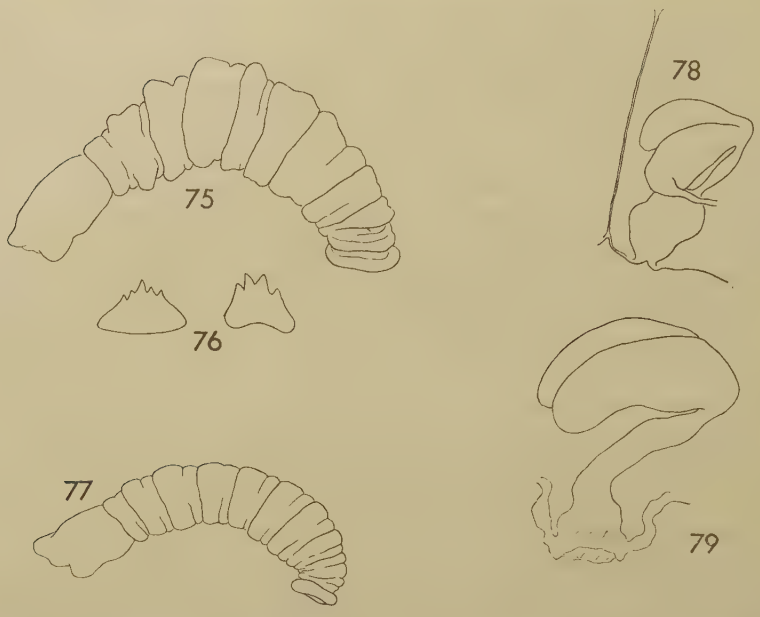
Remarks.—The possibility of any host specificity on the part of this species is negated by the fact that the type series came from a collection of two species of *Orconectes*, the other known material from a collection of two species of *Cambarus*. Presumably the factors influencing the distribution of *demissa* are those of simple geography and water conditions rather than the occurrence of the crayfish hosts.

I cannot, at this time, imagine what might favor the selection resulting in the drastically reduced size of the reproductive systems, unless it be that residence within the branchial chambers of crayfish affords survival with a reduced number of progeny. Perhaps knowledge of the ecology of the species will shed some light on this interesting evolutionary problem.

The name *demissa* (Latin, humble, unimposing, modest) seems appropriate in view of the general form of the animal as well as its very moderately scaled reproductive systems.

Species of uncertain systematic position

Under this heading I include two species which are known to be referable to *Cambarincola*, but which, for one reason or another, cannot



FIGURES 75–79.—Structural details of two species of *Cambarincola*. 75, *C. floridana* Goodnight, body in lateral aspect, camera lucida drawing from holotype; 76, the same, jaws in dorsal aspect, from freehand sketch. 77, *C. gracilis* Robinson, body outline of holotype; 78, the same, male reproductive system of holotype; 79, the same male reproductive system, with bursa everted, paratype from British Columbia.

at present be allocated to a group or even to a section with assurance. The type specimens of both have been studied and drawn; the data on hand are summarized and presented at this time for the benefit of future workers who may be able to collect at the type localities and establish the identities of the names.

Cambarincola floridana Goodnight

FIGURES 75, 76

Cambarincola floridana Goodnight, 1941, Trans. American Microsc. Soc., vol. 60, p. 70.

TYPE SPECIMENS.—Holotype, USNM 20570, from *Procambarus fallax* collected in Taylor County, Florida, by Horton H. Hobbs. This specimen is mounted laterally, but the reproductive system cannot be made out with certainty.

REMARKS.—The bursa of this species is of considerably greater size, in relation to the other organs, than in most other species of the genus. Otherwise the general configuration suggests that *floridana* may be a specialized member of the Philadelphica section.

Cambarincola gracilis Robinson

FIGURES 77–79

Cambarincola gracilis Robinson, 1954, Journ. Parasitology, vol. 40, p. 466, figs. 1–4.—Holt and Hoffman, 1959, Journ. Tennessee Acad. Sci., vol. 34, p. 103.

TYPE SPECIMEN.—Holotype, USNM 26110, from *Pacifastacus klamathensis* collected at Whitman College, Walla Walla County, Washington, by A. G. Rempel. Paratypes: USNM 26111, from the Klamath River, Siskiyou County, California, and USNM 26112, Burnaby, British Columbia.

REMARKS.—This species was described and illustrated in some detail, the account being more meaningful than most of the existing descriptions. Not only the body form and jaws were drawn and discussed, but the form of the reproductive systems as well, and a reasonable comparison was made with *C. inversa* and *C. macrodonta*. It is unfortunate that equal care in the diagnosis of new species was not expended by several of Miss Robinson's predecessors.

I have examined the type material in the U.S. National Museum, and cannot improve upon the original description except to note that the bursa is of the typical cordate *Cambarincola*-form, and not a gradual enlargement of the ejaculatory duct as indicated in Robinson's figure 1. Her figure 3, a reconstruction from serial sections, was made from a worm with everted bursa.

The reduced size of the male sex organs is perhaps of some diagnostic importance, the appearance in situ being reminiscent of that of *C. demissa*. Miss Robinson failed to record the histological appearance of the spermiducal gland and prostate, and, unfortunately, I neglected to note the same detail when examining the type.

A re-examination of material of *gracilis* can readily establish the status and taxonomic position of the species. Assuming that the prostate is not differentiated (it is known to have no terminal bulb), the species will fall into the Mesochorea section and either the Branchiophila group or a new one of its own.

C. gracilis was recorded from ten localities in California, Oregon, Washington, and British Columbia, a relatively extensive range. Yet curiously enough, Goodnight (1959) refers *gracilis* to a category of so-called scarce, localized species in his most recent synopsis, while ranking in the main part of the key some of his own species known from but a single locality.

The paratype from California cannot be studied with respect to the reproductive system. That from British Columbia, however, is well-mounted, and appears to be correctly identified with the holotype.

Drawings made from the holotype and paratype are presented as an aid for future recognition of the species.

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